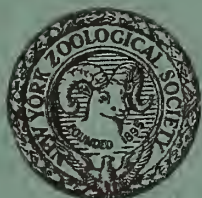


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Neural Adaptations in the Visual Pathway of Certain Heliconiine Butterflies, and Related Forms, to Variations in Wing Coloration¹

S. L. SWIHART

*Department of Biology
N. Y. State University College
Fredonia, New York 14063*

(Figures 1-8)

[This paper is a contribution from the William Beebe Tropical Research Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, West Indies. The station was founded in 1950 by the Zoological Society's Department of Tropical Research, under Dr. Beebe's direction. It comprises 250 acres in the middle of the Northern Range, which includes large stretches of government forest reserves. The altitude of the research area is 500 to 1800 feet, and the annual rainfall is more than 100 inches.

[For further ecological details of meteorology and biotic zones, see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I." by William Beebe, *Zoologica*, 1952, 37 (13) 157-184.

[The success of the present study is in large measure due to the cooperation of the staff at Simla, especially of Jocelyn Crane, Director. The author particularly wishes to acknowledge the invaluable assistance of Dr. Donald R. Griffin, Dr. Michael Emsley, and Mr. John G. Baust].

INTRODUCTION

THE EXPERIMENTS which form the basis of this paper were stimulated by the well-known responsiveness of butterflies to visual stimuli of various colors. Behavioral observations of this phenomenon include those of Eltringham (1933), Ilse (1937), Magnus (1956), and most particularly those of Crane (1955, 1957).

Crane's demonstration of the responsiveness of *Heliconius erato* to orange-red stimuli in feeding and courtship behavior prompted a series of experiments designed to determine the physiological basis of this special sensitivity to long wavelengths. These experiments (Swihart, 1963, 1964, 1965) have demonstrated that: (1) the visual system of *H. erato* includes at least two types of receptors, one maximally sensitive to blue-green and the other peaking in the red (ca. 620 m μ); (2) the receptors interact with each other producing an electroretinogram (ERG) waveform with a distinct color component; (3) specific neural pathways are associated with these receptors. Recordings from the internal chiasma, medulla interna, and the vicinity of the optic nerve demonstrate a spectral sensitivity which indicates a particularly close association between the red receptors and the main pathway of information to the brain.

The behavioral sensitivity of this species seems, therefore, to be related not to any special modification of the receptors, but rather to the development of pathways which "selected" the output from those receptors which transduced information with special biological significance.

The basic hypothesis emanating from these observations was that there was a selective advantage in developing neural mechanisms which demonstrate disproportionate sensitivity to the basic wing coloration, presumably because of the role played by such colors in releasing courtship behavior. This hypothesis invited testing by

¹Supported by grants (GB-2331 and GB-4218) from the National Science Foundation.

conducting experiments on forms other than *erato*, which possessed different wing coloration, to determine how general this mechanism might be, and the degree of adaptive flexibility afforded by such a system. This paper reports the preliminary results of such a comparative study.

METHODS AND MATERIALS

Standard electrophysiological techniques were employed. Intact organisms were rigidly mounted with plasticene as previously described (Swihart, 1963, 1964). Evoked potentials were recorded from the optic lobe with a semi-micro (ca. 500 kohm), 3M KCl filled, glass electrode. On the basis of previous experiments (Swihart, 1965), a technique was developed for placing the electrode almost directly into the medulla interna, via a minute hole in the posterior (occiput) region of the head. Usually only very small additional movements of the electrode were required to obtain the long-latency, negative polarity, response characteristic of the medulla interna (see fig. 15, Swihart, 1965).

In order to ascertain that the preparation was continuing to yield "normal" responses to photostimulation, ERGs were recorded simultaneously with a sub-corneal steel electrode. Experiments were terminated if there was any change in the ERG waveform.

Potentials were amplified with Grass P6 D.C. amplifiers, displayed on a Tektronix four beam 564 oscilloscope, and photographed with a Grass C-4 camera for subsequent measurement.

Photostimulation was accomplished with a laboratory constructed stimulator which, automatically, sequentially introduced a series of 15 narrow-band interference filters into an optical system, and provided a 100 msec. stimulus at each wavelength, at a preset and constant interval, usually about one minute. The stimulus duration was chosen as the shortest which would ensure production of all the components of the ERG (Swihart, 1964).

Preparations were aligned so that the stimulating beam, focused by a microscope objective, illuminated nearly an entire eye. The beam axis was perpendicular to the center of the cornea. Histological studies which have been conducted on a number of the forms selected for this study (*Morpho*, *Agraulis*, *H. sarae*, and *H. erato*), and physiological experiments involving the stimulation of small portions of the eye (of *H. erato*), have not demonstrated any anatomical or physiological differentiation between various regions of the eye.

Peak transmission points of the interference filters were fairly uniformly spaced throughout the visible spectrum from 404 m μ to 709 m μ .

Through the use of a specially-ground, color-compensating filter, and sandwiched gelatin filters, the stimulus energy at each wavelength was held constant ($\pm 20\%$) as determined with an Eppley thermopile.

Equipment was not available for making small, calibrated adjustments in stimulus intensity, hence "spectral sensitivity" (threshold energy) curves were not attempted, rather the electrical magnitude of the response to a standard stimulus of about 5×10^3 microwatts/cm² was determined.

Spectral efficiency curves were constructed by running through the series of 15 filters three times for each preparation. The magnitude of the response to a particular stimulus was evaluated as a percentage of the largest response to any filter in that particular series. The percentage responses to the three successive series were then averaged to produce the curve for a single preparation. The technique of recording the amplitude of the response, seemed justified since the magnitude of the medulla interna response demonstrates a nearly linear relationship to the log of the intensity of stimulation, within the range of intensities studied. In this range, a tenfold increase in white light intensity, produces an increase in response magnitude of about 30%.

Experimental material was normally captured in the wild and maintained in large outdoor insectaries. This technique permitted the selection and testing of only healthy animals.

Wing spectral reflectance characteristics were measured with a Bausch & Lomb "Spectronic 20" spectrophotometer with reflectance attachment. This equipment measures the reflectance of an area approximately 2 mm x 8 mm. Only specimens which appeared to be newly emerged were used for such determinations.

It will doubtlessly be noted that the number of specimens of each species investigated is frequently very small. It is hoped that this will be understood as related to certain problems which were encountered, including: (1) the physical difficulty of capturing healthy specimens of certain elusive and rare species, notably *Philaethria* and *Morpho*; (2) the extremely delicate nature of these organisms which results in their entering a state of "shock" if handled roughly. This condition is evidenced by abnormal behavior, including strong positive phototaxis, and highly aberrant evoked potentials, usually accompanied by very large (ca. 5 mV) low-frequency spontaneous discharges; (3) the necessity of limiting the observations to only those individuals which produced strong "day" type electroretinograms (Swihart, 1963); (4) the problems in placing the micro-electrode into the

intact organism in such a manner that it reaches the very limited region near the medulla interna, which yields the long-latency negative potentials, without inducing operative trauma, and its resultant massive spontaneous activity.

Six species of butterflies were selected for this study. All belong to the family Nymphalidae. Four are members of the subfamily Heliconiinae, while the Morphinae is represented by one form (*Morpho*), and the Nymphalinae by *Victorina*.

Studies were begun on *Heliconius sarae* because of its fairly close relationship with the subject of previous experiments, *H. erato*. In Trinidad, *erato* is a small black butterfly (2½" wingspread) with bright red spots on the forewings. *H. sarae* is, in many respects, a very similar butterfly, with the most obvious difference being the substitution of a pair of bright yellow bands on each forewing. In addition there is a moderately strong blue iridescence on the hind wings.

Heliconius ricini was chosen because it offered an "intermediate" color pattern to *sarae* and *erato*. In *ricini*, the black "base" color of the wings is broken by forewing yellow bands (as in *sarae*), but a large red hindwing spot is also present. *H. sarae* and *ricini* are the most closely related of the forms tested. Both belong to the same species-group as discussed by Emsley (1965).

The third form chosen, *Agraulis vanillae*, was selected because its color pattern is similar to that of a number of other primitive Heliconiinae. That is to say, the wings are predominantly bright orange in color.

Even a cursory glance at the variety of wing color patterns characteristic of the Heliconiinae demonstrates a single basic plan. This is a long-wavelength color with a contrasting dark brown or black. It can be seen that the aforementioned forms are representative of this basic pattern. However, for purposes of investigating the physiological adaptations of the visual pathway, it seemed desirable to investigate forms with an unusual wing coloration. Initially, it was hoped that studies could be made on the rare, predominantly green heliconiine, *Philaethria dido*; however, only a single healthy specimen of this species was obtained, and observations were extended to the very similarly marked nymphalid, *Victorina steneles*.

Finally, to further extend the variety of wing colors, observations were made on the blue-winged *Morpho peleides*.

The results of the observations on each species will be considered separately.

RESULTS

Heliconius sarae thamar Hubner

A total of eight individuals that were tested yielded acceptable responses, i.e., long-latency negative potentials. A ninth individual producing such responses became erratic before the experiment was completed; however, its performance in the early stages of the experiment gave a clear indication of its sensitivity.

It was found that the spectral efficiency curves produced by these individuals were far from being identical to each other. Examination of the curves revealed that they could be separated into two distinct types, with each category being fairly homogeneous. Figures 1 and 2 show these two types of curves. Four individuals demonstrated a sensitivity peak in the orange-red portion of the spectrum (ca. 620 mμ); the remainder were maximally sensitive to green.

In spite of the small sample size, the differences between these two curves is so great that there is no statistical basis for doubting that they represent two distinct populations. Thus, for example, one obtains by comparing the percentage responses at a single wavelength (523 mμ), at value of 4.78, with a $n = 7^*$. The probability that the responses represent different populations is thus greater than 0.995. If this analysis is carried to additional points on the spectra, no reasonable doubt can remain.

The red-sensitive curve peaks at 620 mμ, and in this respect is very much like the responses recorded from *erato*. However, there is a difference between the two forms in their sensitivity to shorter wavelengths. Thus, the response of *sarae* to stimulation with short wavelengths is, on the average, considerably greater than *erato* (Fig. 2).

Figure 3 shows the spectral reflectance curves of the *erato* red pigment, and the *sarae* yellow. It can be seen that the yellow color could actually be described as "blue negative," since it actually reflects about the same amount of red as does the *erato* pigment. If one, therefore, considers the difference between these colors in terms of a greater reflectance of mid and shorter wavelengths, there is a parallel in the differences between the reflectance and spectral efficiency curves in the two forms.

$$^* \text{ where } n = \frac{\left(\frac{s_1^2}{N_1} + \frac{s_2^2}{N_2}\right)^2}{\left(\frac{s_1^2}{N_1}\right)^2 \frac{1}{N_1 + 1} + \left(\frac{s_2^2}{N_2}\right)^2 \frac{1}{N_2 + 1}} - 2$$

which is an approximation of a longer formula given by Welch (1947).

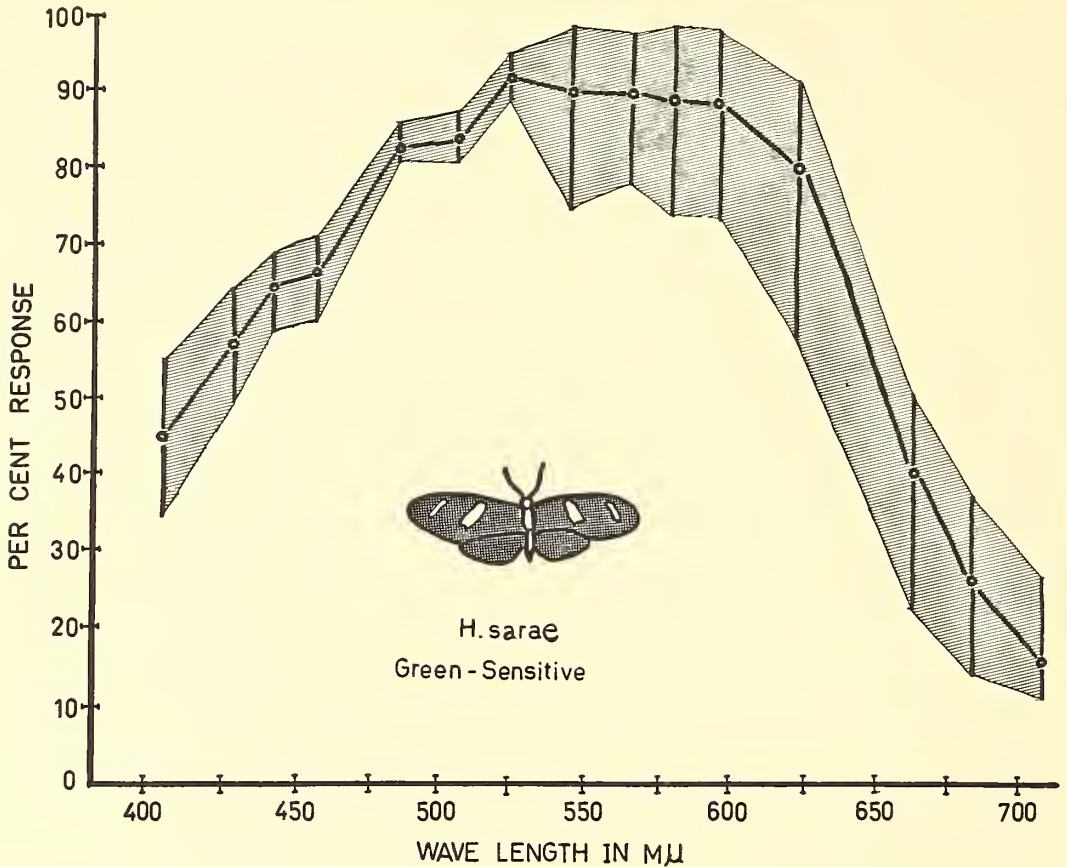


FIGURE 1.

One of the two types of spectral efficiency curves found to be characteristic of *Heliconius sarae*. Measurements were based upon the magnitude of long-latency, summated potentials of negative polarity in the vicinity of the medulla interna. See text for details of technique. Vertical bars indicate the limits of observed variability between individuals, i.e., the maximum and minimum responses to any given wavelength. Illustration is a semi-diagrammatic representation of the dorsal surface; unshaded portions correspond to the areas of yellow pigmentation. Shaded area represents the distribution of near black wing pigmentation. Unless otherwise noted, all subsequent diagrams are to the same scale.

The other type of spectral efficiency curve was recorded with the same frequency as the red-sensitive one (four of each, with the previously mentioned ninth being red sensitive). It would appear that the sensitivity of these organisms was largely determined by the green-sensitive receptor system with a slight and variable skew produced by the presence of the red system.

At this time it is impossible to identify the factors which contribute to the differences between these two types of individuals. All the organisms were tested at approximately the same time of day (late morning), and demonstrated similar "day" type electroretinograms. Three males and one female yielded the red-sensitive curve, while three females and one

male produced the green curve. The age of the individuals was not known since they were all wild caught specimens.

It should be remembered, however, that behavioral observations on butterflies have demonstrated rather dramatic shifts in the colors to which they will respond, depending upon their physiological state. Thus, Ilse (1937) showed that while *Pieris brassicae* selected red, yellow or blue colors in its feeding behavior, it became specially responsive to the color green when involved in egg-laying behavior. It may well be that such shifts in spectral sensitivity represent a measurable index of the rather abstract concept of "physiological state."

Heliconius ricini (L.)

A total of eight specimens of this species pro-

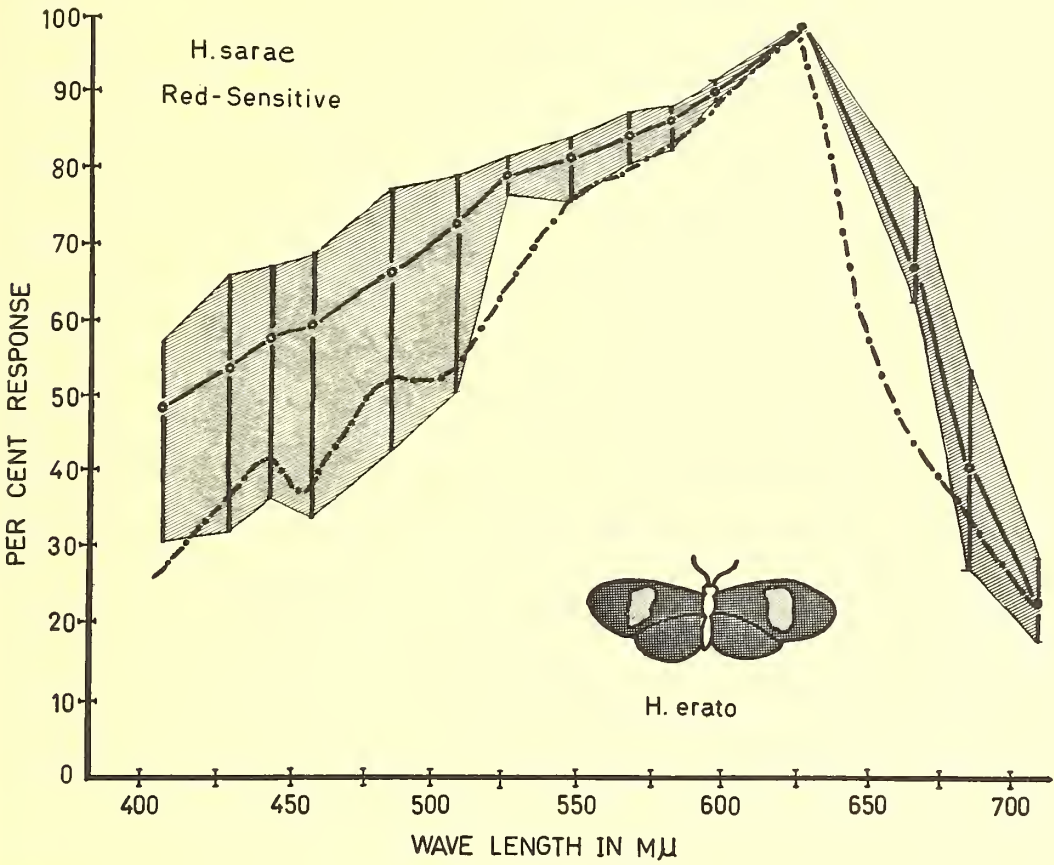


FIGURE 2.
Alternate type of spectral efficiency curve that may be recorded from *Heliconius sarae* which demonstrates far greater sensitivity to long wavelengths than does the curve in Figure 1. Also included in the figure, for purposes of comparison, is the comparable average spectral efficiency curve recorded from four individuals of the species *Heliconius erato* (dot-dash-line). Also figured is the distribution of red pigmentation in the forewings of *H. erato*.

duced acceptable responses. In spite of the fact that the wing coloration of this form can be considered to be intermediate between *sarae* and *erato* (i.e., has both red and yellow markings), the responses were entirely similar to *sarae*. Thus three of the individuals yielded spectra peaking in the red (Fig. 4) (620 mμ), with no significant differences from the *sarae* red-sensitive curve. One of the specimens tested was most interesting in that the nature of its response changed during the course of the experiments. The responses to the initial filter series indicated a maximum sensitivity to red. A gradual change took place, without any apparent change in the waveform of the response, so that by the time the organism was stimulated by a fourth series of filters, the response was plainly maximally sensitive to green light.

The remainder of the organisms tested produced the non-specific green-sensitive curve.

Agraulis vanillae vanillae (L.)

Five specimens of this primarily orange-colored butterfly produced acceptable responses. The averaged responses of these individuals produced a curve which is distinctively different from any which had been previously recorded (Fig. 5). In many respects, this spectrum can be considered to be entirely intermediate between the two *sarae* spectra. Thus, *Agraulis* demonstrates a curve peaking in the orange, less sensitivity to short wavelengths than the *sarae* green curve, and less sensitivity to long wavelengths than the *sarae* red curve. These differences are so great that there is little or no overlap of even those responses demonstrating the

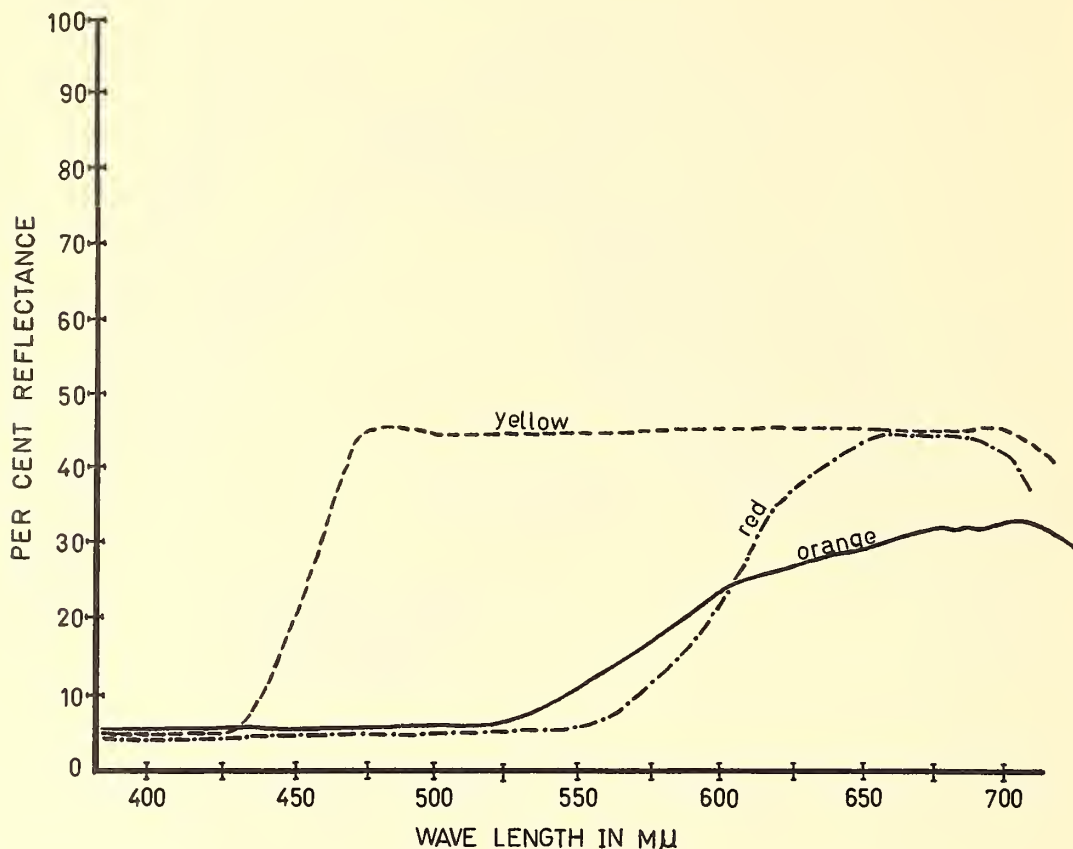


FIGURE 3.

Spectral reflectance characteristics of various heliconiine wing pigments as measured against a magnesium carbonate standard. Intact wings were mounted on a nonreflective backing before being inserted into the spectrophotometer. No differences in reflectance exist between similar appearing areas in the various species, e.g., *erato* and *ricini* red are identical.

greatest variance from the mean in most of the aforementioned portions of the spectrum.

It will be noted that, like *erato*, only a single type of response was recorded from this species.

Philaethria dido dido Clerck and *Victorina steneles* (L.)

It was hoped that observations could be made on the green-winged heliconiine *Philaethria* as it would provide a form with a markedly different wing coloration. Unfortunately, not a single wild specimen could be obtained. Several eggs were located, however, and a single healthy specimen was raised in the laboratory. Testing of this individual did indeed produce responses showing a distinctive peak in the green. Regrettably, no additional specimens were available to confirm these observations. Because of the shortage of *Philaethria*, it was decided to make observations on the remarkably similar nympha-

lid *Victorina*. These forms are so similar that they can be easily confused. The resemblance is much more profound than mere superficial appearance. Both forms have developed their green coloration by a most interesting technique. In the green areas of the wings, the scales are either much reduced, or missing, and the pigmentation is within the wing membranes. The coloration itself appears to be due to the presence of two pigments. One of these absorbs in the blue (i.e., appears yellow) and can be extracted with ether, leaving an insoluble blue compound behind (Fig. 6). It seems likely that this unusual wing coloration is due to haemolymph pigments (Hackman, 1952) since *Victorina*'s blood and eggs are both bright grass-green.

Four specimens of *Victorina* were tested and found to resemble *Philaethria* in visual mechanisms as well as in pigmentation. Figure 7 shows

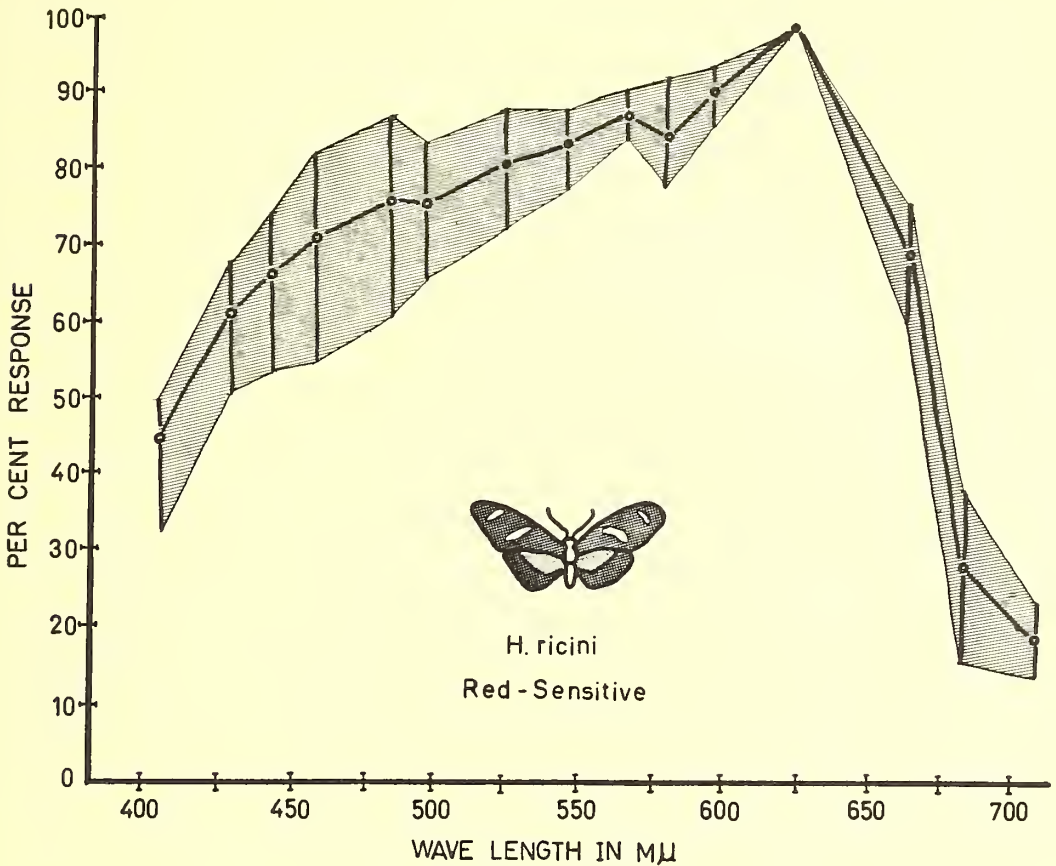


FIGURE 4.

One of the two spectral efficiency curves characteristic of *Heliconius ricini*. Note the great similarity to Figure 2. The other type of curve is similar to the *sarae* "green-sensitive" curve illustrated in Figure 1. Unshaded areas of illustration correspond to the distribution of the yellow pigment, while the lightly shaded area represents the hind-wing red spots.

the luminosity curve produced by these individuals which clearly peaks at about 565 mμ. There can be no doubt that this curve is distinctly different from the green-sensitive curve of *sarae*. At virtually every wavelength longer than the 565 mμ maximum, the *Victorina* responses are so greatly reduced that there is very little, if any, overlap with even those *sarae* showing the greatest deviation from the mean.

The curve recorded from the single *Philaethria* was entirely similar to that produced by *Victorina*, and fell well within the limits of *Victorina* variability.

Morpho peleides insularis Fruhstorfer

It was considered advisable to make tests on a form with a primarily blue wing coloration. Since there is no such heliconiine in Trinidad, it was decided to utilize the large blue-violet

morphine *Morpho peleides*. This butterfly is well known to show a special sensitivity to the color blue. For many years, professional collectors have used this fact to assist in the capture of this elusive species, with its highly prized iridescent physical coloration.

Two specimens of this species were fully tested for spectral efficiency. The electrical responses produced by these organisms were found to be so different from the responses of the heliconiine that direct comparison is difficult. The electroretinograms show none of the complexities, described in detail for *erato* (Swihart, 1964). The waveform consists of a B wave, followed by a uniform, sustained negativity during illumination. All the ERG components usually associated with the red-sensitive receptor, such as the "dip" following the B wave, and "off" effect, are totally absent.

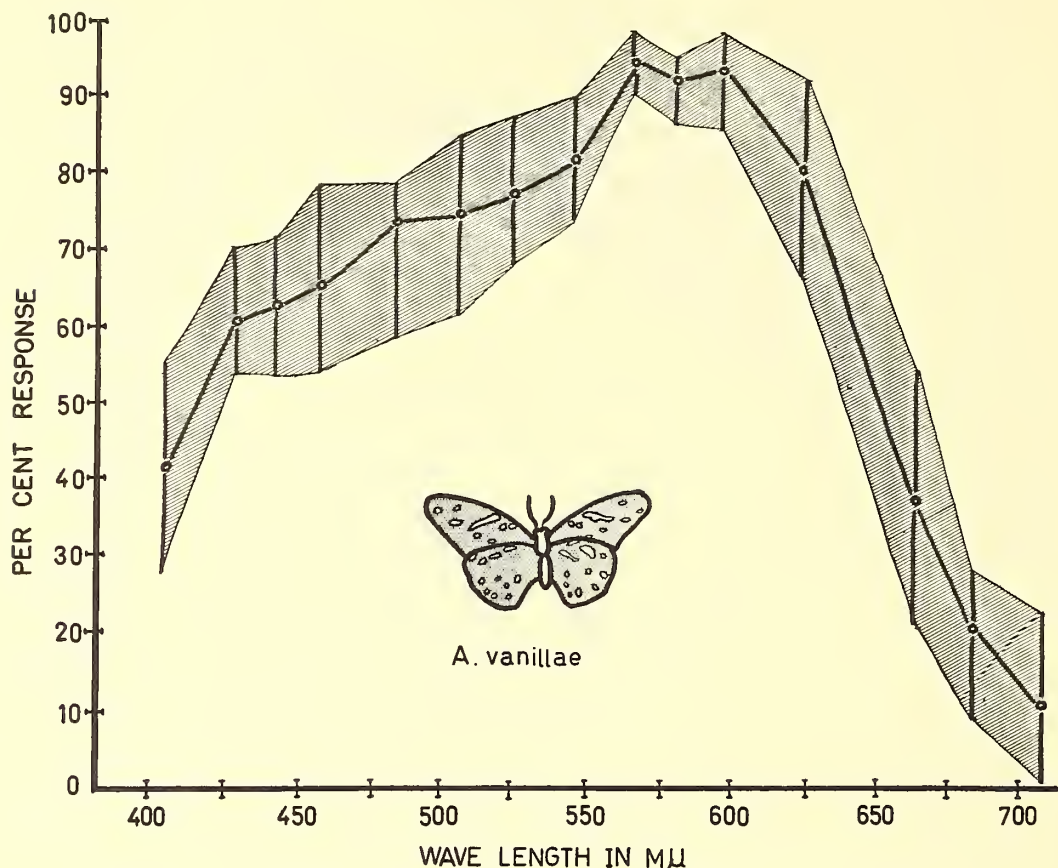


FIGURE 5.

Single type of spectral efficiency curve recorded from five specimens of *Agraulis vanillae*. This species is a nearly uniform orange color (light shading), with numerous small black (unshaded) spots on the wings.

These differences in the ERG waveform are reflected in differences in evoked potentials, as recorded with micro-electrodes. Unlike the heliconiine, it was found that the evoked potentials were generally directly proportional in magnitude to the size of the ERG. The spectral efficiency of these effects, as measured by the ERG B wave magnitude, is indicated by Figure 8. The skew of this curve towards the blue, with its peak at about 485 mμ is both obvious and strikingly different from the curves produced by the heliconiine.

Two additional specimens of this species were tested in the course of work preliminary to the experiments which form the basis of this report. Full spectral efficiency curves, as determined by the standard technique, were not calculated for these individuals. They did, however, appear to demonstrate the same ERG waveform and great sensitivity to short wavelengths.

DISCUSSION

It is unfortunately true that the fundamental mechanisms of color vision remain largely unexplained. This lack of knowledge is particularly apparent in the case of invertebrates, where even the method of coding color information has not been identified as has been done for certain vertebrates (e.g., Wagner *et al.*, 1960; Muntz, 1962).

Recent microelectrode studies (e.g., Horridge *et al.*, 1965) have revealed a vast complexity in discharge patterns in the insect visual pathway. There is, however, some question as to the adequacy of such single fiber techniques to record from those fibers most intimately involved in the highest forms of behavior. There can be no doubt that these techniques tend to select large-diameter fibers. Such neurons have been repeatedly demonstrated to be associated with flight or escape reactions, and hence can hardly be

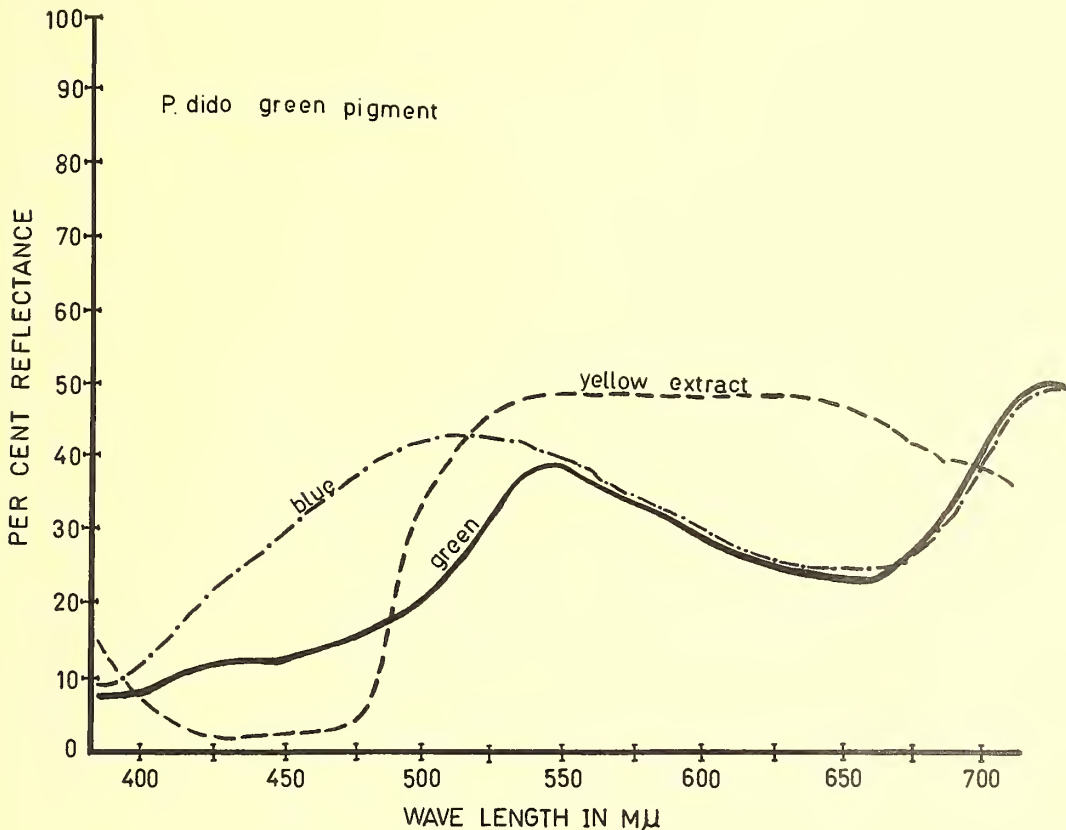


FIGURE 6.
Reflectance characteristics of the green wing areas of *Philaethria dido* and *Victorina steneles*. Since the scales are much reduced, or absent in these regions, they are quite translucent and reflect poorly. Because of this fact, the wing reflectance was measured with a white backing. This technique increased the height of the curve without altering its shape. Solid line illustrates the characteristics of the natural wing coloration. Dot-dashed line indicates the reflectance of the wings after being extracted with ether. Dashed line indicates the transmittance of the yellow-colored extract. The height of this curve was adjusted by plotting $\frac{\% \text{ transmittance}}{2}$.

considered as representative. For these reasons semi-microelectrodes have been employed in the current study, as it seems not unlikely that a "summed" response reflects the nature of the nervous activity with somewhat less bias.

In this connection, it should be remembered that it was demonstrated (Swihart, 1965) that there are fibers with discharge patterns related to the magnitude of such summated potentials. Thus, the curves presented in this report reflect the discharge frequency (and hence the total number of spikes per stimulus of standard duration) of at least some of the neurons in the visual pathway.

Recently, Goldsmith (1965) has given evidence that spectral sensitivity curves derived

from summated (ERG) potentials must be carefully interpreted if screening pigments are present. Such problems are not encountered in the genus *Heliconius*, where the only pigmentation appears to be a nearly black substance, localized in granules within the iris pigment cells.

In the case of *Agraulis* and *Victorina* there is a light orangish pigmentation within the corneal cuticular layer. This pigmentation does not appear to penetrate to the deeper layers of the eye, and hence probably could not produce the effects described for *Musca*. However, the role of such accessory pigments deserves further investigation.

A careful analysis of the techniques employed in these experiments may suggest that they lack

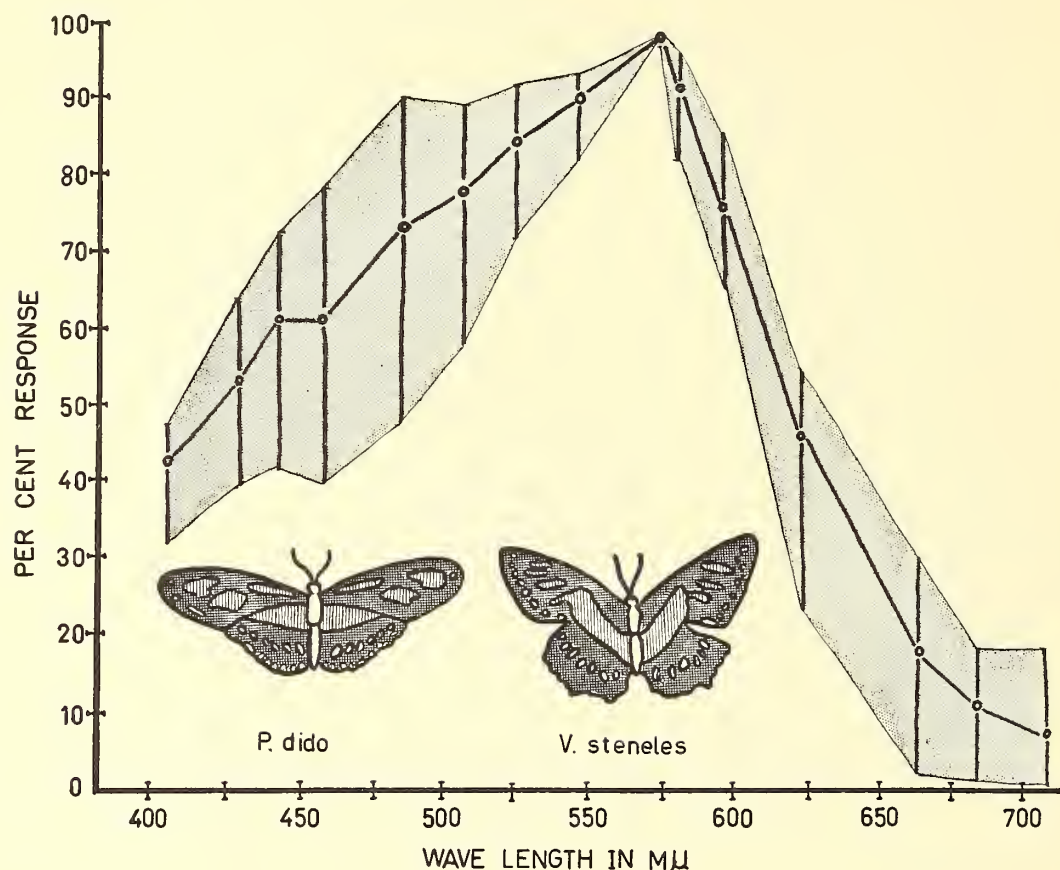


FIGURE 7.

Spectral efficiency curve recorded from four specimens of *Victorina steneles*. The single specimen of *Philaethria dido* demonstrated a similar sensitivity. Lightly shaded areas of illustration represent the distribution of the green coloration, as opposed to the dark brown-blackish pigmentation.

some of the controls commonly employed in the investigation of primary visual events. It must be remembered that this is primarily a comparative study and that the techniques employed on one form were identical to those used on the others. Thus, while it may not be possible to interpret the results as representative of photopigment absorption spectra, they are indicative of real differences which exist between closely related forms.

It is reasonable to enquire as to the origin of these differences.

Analysis of the magnitude of the electroretinograms, in a method analogous to that described in this paper, produces spectral efficiency curves with no significant differences between the various Heliconiinae. In every case the curves resembled that described for *H. erato* (Swihart, 1963). This fact strongly suggests that the varia-

tions between forms cannot be related to differences in the nature of the photopigments.

Alternatively one might suggest that the variations in sensitivity are due to differences in the relative numbers of several different types of receptors, (e.g., *Calliphora*; Autrum & Burkhardt, 1961). However, an explanation based upon such a rigid mechanism seems inconsistent with the type of variability observed in *sarae* and *ricini*.

For such reasons, it seems most reasonable to interpret the observed variations in the summated responses to various colors, as a neural phenomenon.

Turning to a consideration of the spectral efficiency curves themselves, we find a most interesting series in the responses of *Agraulis*, *sarae* and *erato*. In considering these forms, it is worth noting that casual behavioral observations

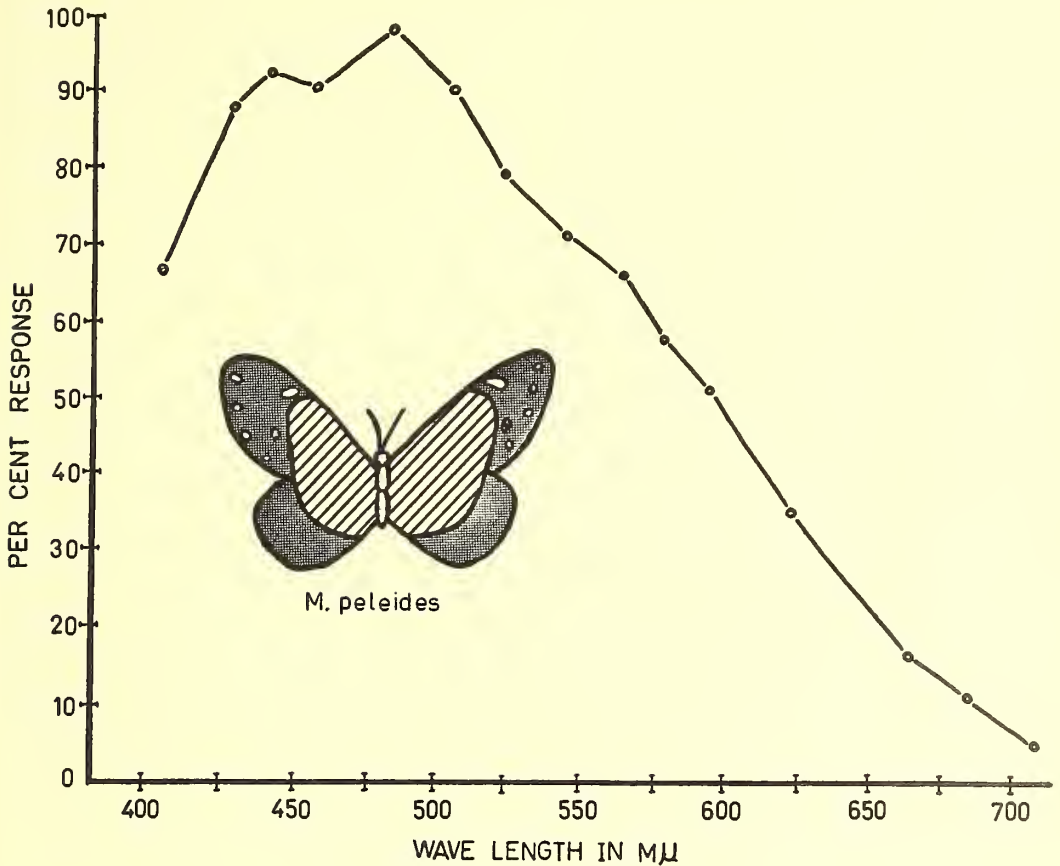


FIGURE 8.
Average spectral efficiency curve derived from two specimens of *Morpho peleides*, as determined by the ERG B-wave magnitude. Very little variability between the individuals was observed. Illustration is at reduced scale. Central (hatched) areas of wings is iridescent blue, with contrasting brown-black margins.

by the author have indicated that consistently stronger behavioral responses to specific colors are produced by the species with the red and orange markings. In the case of *sarae*, attempts to demonstrate a behavioral sensitivity to yellow or red have, as of this time, produced no positive responses in courtship (Crane, pers. com.). This condition would seem to have a physiological correlate in the existence of the two types of spectral efficiency curves recorded from this form, as opposed to the uniformity which characterizes the two other species.

It would appear that considerable significance can be attached to the variability between individuals producing each of the two different *sarae* curves. Each of the curves demonstrates a highly asymmetric distribution of the degree of variability, which would hardly be expected on the basis of a "normal" distribution of variance. The most likely interpretation of these

curves would seem to be that the green-sensitive curve reflects the activity of a visual system responding primarily to the sensitivity of a blue-green sensitive receptor, with a small and variable contribution by a red-sensitive system. On the basis of such an interpretation, the short wavelength portion of this curve (400-525 mμ) would probably reflect a portion of the inherent sensitivity of the receptor system. Conversely, the red-sensitive curve illustrates a high degree of variability only at wavelengths below 525 mμ. This would seem to imply that the system is responding primarily to a red-sensitive receptor (maximum 620 mμ), with a small and variable contribution by the blue-green system. These two maxima observed in *sarae* are the same as those reported for *erato* (Swihart, 1964).

By comparison, the single type of spectral efficiency curve characteristic of *Agraulis* demonstrates a fairly uniform variability through-

out the spectrum. This would seem to indicate that the mechanism is not "dominated" by a single receptor system, but rather reflects the neural summation of the activity in several receptor types. Indeed, the peak of such a curve may not correspond to any specific type of receptor, but, rather, indicate a region where the overlapping sensitivity of two receptors "summates" to produce an "artificial" peak. It is, therefore, interesting to note that the peak of the *Agraulis* curve lies midway between the maxima of the two receptors postulated for *sarae* and *erato*.

Extending our analysis to the other forms studied, we find that *ricini* is similar in all respects to *sarae*. This is not particularly surprising when one considers both the extremely close phylogenetic relationship between the two forms (Emsley, 1965) and the basically similar wing coloration (i.e., forewing yellow bands).

Turning to the two similar green forms, *Philaethria dido* and *Victorina steneles*, we find several significant differences from the species previously considered. First is the rather obvious shift in the peak from the 528 m μ region to about 570 m μ . The very small variance between individuals at the peak of the curve suggests that this is probably due to a difference in receptors rather than a mechanism such as that postulated for *Agraulis*.

The second remarkable feature of the *Victorina* curve is the extremely attenuated response to long wavelengths. It seems most unlikely that the orange color of the cornea could be responsible for the diminished responsiveness to long wavelengths. While it is possible that this portion of the curve represents the sensitivity of the receptors, it seems much more probable that some other mechanism is involved (e.g., inhibition by a red receptor system).

It is difficult to extend the preceding type of analysis to *Morpho*, since the responses of this form (ERG and neural) are so different from the preceding forms as to make a direct comparison difficult, if not impossible. Regardless of the final interpretation of the nature of the visual mechanisms of this form, it is clear that virtually all the recorded responses demonstrate a maximum sensitivity to the blue portion of the spectrum. It is obvious that this organism must possess a blue-sensitive receptor. The question is, therefore, whether this represents a unique type of receptor. The neural responses of the other forms have given but little indication of any special sensitivity to short wavelengths. Only *Victorina's* neural spectral efficiency curve demonstrates the type of variability between individuals which could be interpreted as being

clearly indicative of the activity of a blue sensitive system. On the other hand, spectral efficiency curves based upon the ERG B-wave demonstrate a rather considerable sensitivity to short wavelengths. This is true even in the case of the primarily red-sensitive *erato* (Swihart, 1963). It seems possible, therefore, that such a system may be fairly commonly distributed among the Nymphalids; however, evolutionary adaptation has resulted in its contributing little or nothing to the excitation of the information pathway in the vast majority of species where the primary wing coloration is in the long wavelength portion of the spectrum.

To conclude this discussion, it is interesting to speculate as to the evolutionary forces which have contributed to the development of the weak and variable responses characteristic of the forms with the yellow forewing bands, i.e., *sarae* and *ricini*. In considering this problem, one must remember that there are two important factors which have played a role in the development of butterfly wing coloration. These are: protective (warning or mimetic) coloration and the conservative force of sexual selection. These two forces are frequently antagonistic. In fact, the opposing pressures of these two factors are believed (Brower, 1963) to have produced the multiple cases of sexual dimorphism in wing coloration found in butterflies.

As previously noted, many of the primitive Heliconiinae are primarily orange in color. This coloration appears to be due to a pterin pigment (Baust, 1967). A small modification of this molecule has produced the erythropterin pigmentation found in the red spots of *erato*, etc. It seems not unlikely that this refinement of the chromophore, which has produced a coloration with greater purity, has allowed the refinement of highly specific behavior patterns based upon the releasing value of this striking color.

On the other hand, the yellow pigmentation of *sarae* and *ricini* represents the development of an entirely new type of pigment (an amino acid, Brown, 1965) probably in response to some other pressure. It is certain that these forms have not lost the ability to synthesize a pterin pigment since almost all the Heliconiinae demonstrate minute red spots at the base of the forewing. Employment of the yellow pigment vice the red is hard to explain in terms of sexual selection since the low color purity of this pigment would make an inherently poor sign stimulus. On the other hand, the yellow reflects about 207% more light in the visible spectrum than does the red. It seems certain this more brilliant pigmentation is considerably more effective as warning coloration. The species has had to ac-

commodate to this increased emphasis on warning coloration with a lessened dependence on wing coloration as a courtship releaser. This change appears to be reflected in the less specific neural adaptation of the visual pathway to the organism's wing coloration.

It must be admitted that many of the ideas which have been put forth must remain in the category of speculation. To some extent, this seems to be an inherent penalty for attempting to penetrate the perceptual world of another species.

SUMMARY

Specimens of six species of butterflies were examined using standard electrophysiological techniques. Spectral efficiency curves were constructed for each species. For five of the species, this was done on the basis of the magnitude of long-latency, negative polarity, summated potentials, associated with the activity of higher order neurons in the vicinity of the medulla interna.

Two species with yellow forewing spots (*Heliconius sarae* and *H. ricini*) produced similar results, i.e., individuals yielded one of two types of curves, one a non-specific curve peaking in the green, and another peaking in the red, with a shape very similar to the spectral reflectance of the yellow wing pigmentation. The orange butterfly, *Agraulis vanillae*, produced a single type of curve peaking in the orange. The two green butterflies, *Philaethria dido* and *Victorina steneles*, produced curves peaking in the green. The blue butterfly, *Morpho peleides*, produced very different electrical responses. The electroretinogram did not demonstrate the components, which in the preceding forms, are associated with a red-receptor system. The spectral efficiency curve based upon *Morpho*'s ERG B-wave demonstrated a maximum in the blue.

On the basis of these observations, and previous studies of a form with red markings (*Heliconius erato*), it is suggested that butterflies possess a neural mechanism which "selects" the output from various receptors in such a manner so as to make the visual system respond maximally to stimulation with colors approximating the wing pigmentation.

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2

Preliminary Studies on The Isolation of Pterins from the Wings of Heliconiid Butterflies¹

JOHN G. BAUST²

Department of Biology
State University College
Fredonia, New York

(TEXT-FIGURES I-IV)

[This paper is presented as a portion of a series of studies on the Heliconiid butterflies which have been supported by the National Science Foundation and organized by Jocelyn Crane. The focal point of these studies has been the William Beebe Tropical Research Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, W.I. The station was founded in 1950 by the Zoological Society's Department of Tropical Research under the late Dr. Beebe's direction.]

[The success of the present study is in great part due to the invaluable aid rendered by both Miss Crane, director, and Dr. M. G. Emsley, who so graciously contributed many of the specimens needed. The author is particularly indebted to Dr. Jerome H. Supple, Department of Chemistry, and Dr. Stewart L. Swihart, Department of Biology, both of the State University College, for their advice and keen interest in the study. The author wishes to gratefully acknowledge the gifts of samples of erythropterin, xanthopterin and rhizopterin from Dr. E. L. Rickes, Merck and Co., Inc., Rahway, New Jersey].

INTRODUCTION

PTERINS HAVE BEEN isolated from a variety of organisms, e.g., Tschesche & Vester (1955) isolated erythropterin from *Mycobacterium lacticola*, Lecercq (1950) and

Schöpf & Becker (1933) from Hymenoptera, Goto (1963) from Amphibia, and Forest & Mitchell (1954) from *Drosophila*, to mention but a few. Pterins have also been isolated from the wings and eyes of various Lepidoptera (Pfleiderer, 1962; Schöpf & Becker, 1933). However, these studies have been limited to a few moths and butterflies of the family Pieridae. Essentially, this was due to the fact that it has been generally believed that pterins existed only within these groups of Lepidopterans (Ford, 1947; Ziegler-Günder, 1955). As a result of this study, however, it has been demonstrated that at least two Heliconiid butterflies contain pterins as their principle wing pigment.

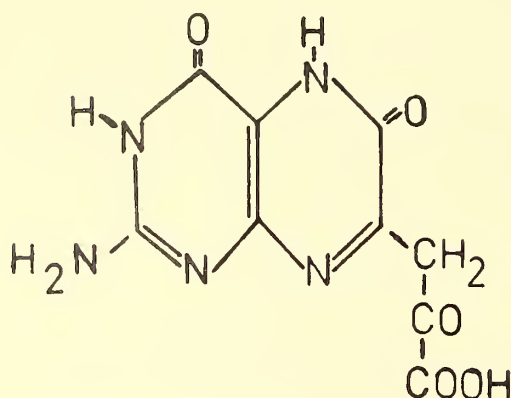
Analysis of the red wing patches of *Heliconius erato adanis*, a black, neo-tropical butterfly with two distinct red spots, has led to the identification of erythropterin (Text-fig. I). Its chemical structure has been described by Purman & Eulitz (1948), Fieser & Fieser (1963), and Tschesche & Korte (1951), and its properties by Fox (1953) and Albert (1954). A second pterin has been detected in the wings of the orange Heliconiid, *Colaenis julia*, but has not yet been identified.

METHODS AND MATERIALS

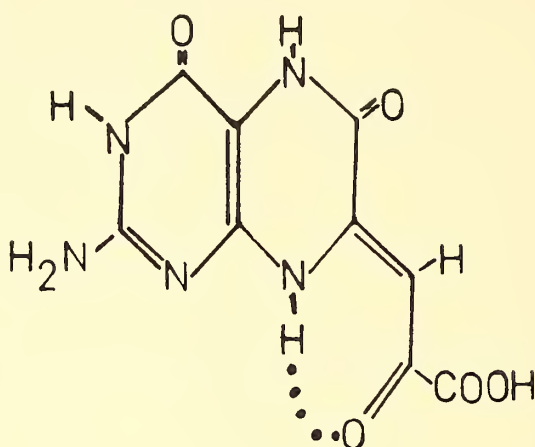
The red pigmented regions of the wild caught *Heliconius erato* were removed. They were then defatted with ethyl ether in a Soxhlet apparatus, and the pigment extracted in a crude form with methanolic HCl, evaporated and redissolved in

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²The author's present address is the Department of Physiology, Downstate College of Medicine, State University of New York, Brooklyn, New York.



ERYTHROPTERIN



TRICYCLIC FORM

TEXT-FIG. I. The proposed bicyclic and tricyclic structures of erythropterin.

methanol. Since only minute quantities of the pigment were contained within the wing portions used, identification was initially limited to paper chromatographic techniques. Whatman filter paper #1 was used, and chromatograms were run in a butanol: acetic acid: water (4:1:5) solvent system.

Ultra violet and visible spectra of the above samples were recorded on a Beckman DK-2 Spectrophotometer.

RESULTS

Initial experiments demonstrated that the physical and chemical properties of the pigment extract were consistent with those commonly attributed to pterins (Cromartie, 1958). The pigment was found to be insoluble in cold water and most organic solvents, was degraded by oxidation, and was melted with difficulty. It was soluble in most acidic and basic media. These observations suggested a more precise identification on the basis of paper chromatography and spectrophotometric comparisons with known pterin samples.

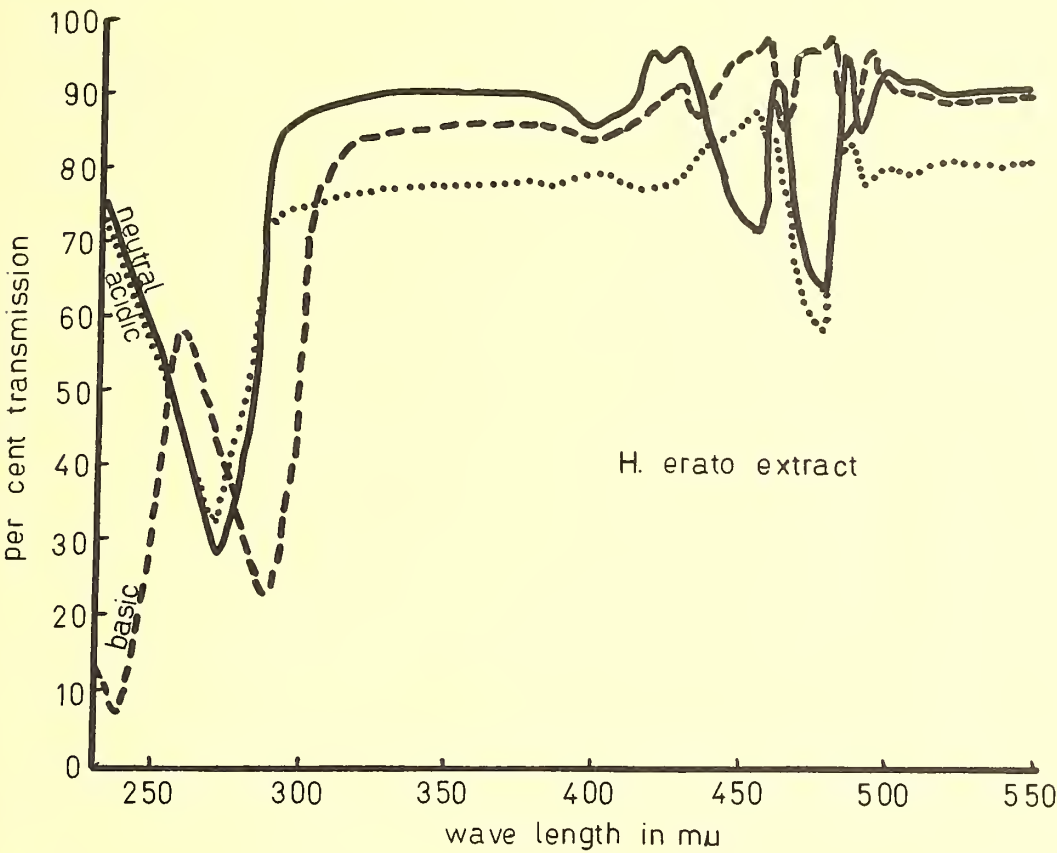
Chromatograms of the crude pigment extracted with methanolic HCl yielded two fluorescent spots with the previous mentioned solvent mixture. The first had a pink fluorescence and an R_f value of 0.33. These results were then compared with chromatograms obtained from what is believed to be pure erythropterin (Table

2)³. The chromatograms of the known and unknown material were found to be identical in R_f values and in fluorescence for both sets of spots. The erythropterin's lower spot compared favorably with the value obtained by Good & Johnson (1949).

The wing pigment and erythropterin spots were analyzed spectrophotometrically, while separately and individually eluted with methanol from the paper. Strikingly similar spectra were obtained in both the visible range (350-550m μ) and in the ultra violet range (230-350 m μ) for all spots. The principle peaks were at approximately 272, 458, and 490 m μ (Table 1 and Text-figs. I & II). It should be noted that the upper and lower spots resulted in all but identical spectra, with only minor differences within the visible range. The lower erythropterin spot (Good & Johnson, 1949) is thought to be the bicyclic form, while the upper spot may be a tricyclic isomer.

A second Heliconiid, *Colaenis julia*, was investigated briefly in an attempt to determine the nature of its pigment. The spectral and chromatographic data (Table 2) obtained from this study showed that the orange color is due essentially to a pterin. The structure of this particular

³Both the rhizopterins and xanthopterins were compared in the same manner as the erythropterin and wing pigment.



TEXT-FIG. II. Ultra violet-visible spectra of the pigment extracted from *H. erato* with methanolic HCl and analyzed in a methanol solvent. Refer to Table I for numerical data for acid-base additions.

TABLE I. ULTRA VIOLET AND VISIBLE SPECTRA*
(CH₃OH solvent)

	Methanolic HCl extract	Erythropterin
Neutral**	273	270
	458	459
	480	481
	490	490
Plus 5% NaOH	235	235
	285	285
	462	463
	485	485
Plus 5% HCl	499	498
	272	270
	459	457
	480	...
	492	490

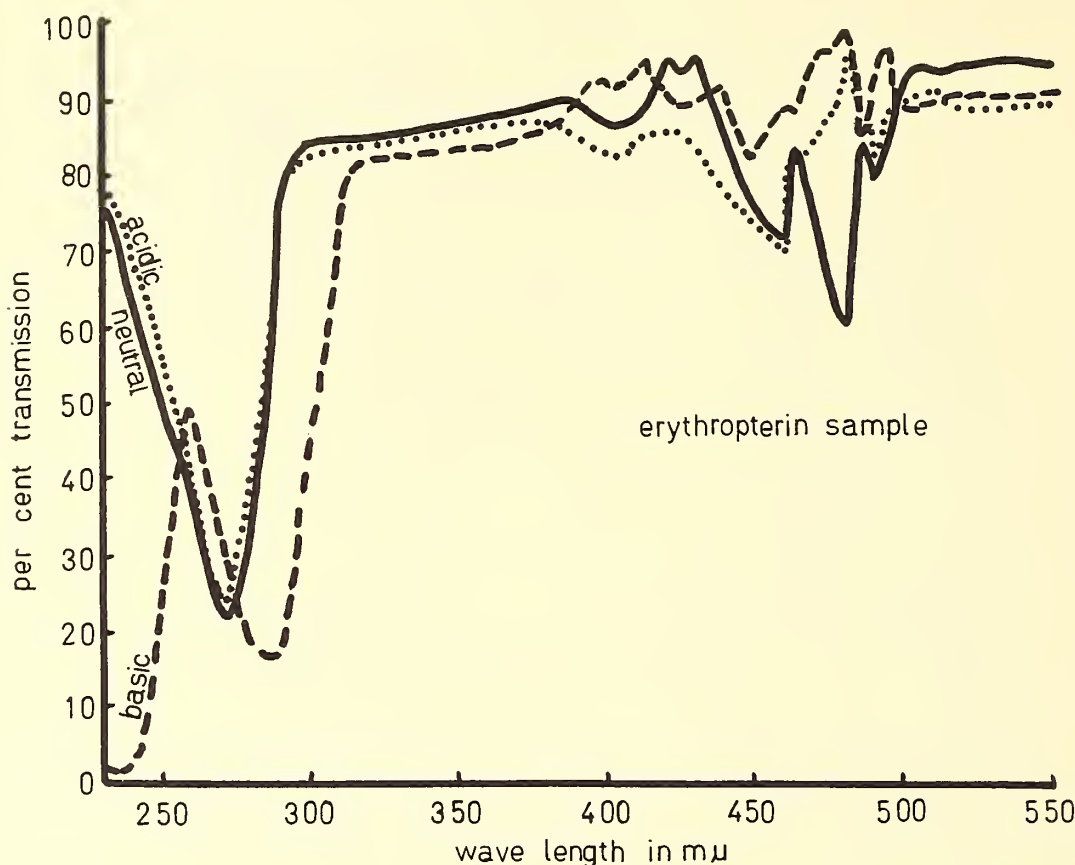
*wave length in mμ

**This is the respective order of the additions of NaOH and HCl.

TABLE 2. RELATIVE R_f VALUES OF PIGMENTS
STUDIED. (Solvent—Butanol:Acetic
Acid:Water, 4:1:5)

Compound	R _f Value
<i>H. erato</i> pigment (extracted with methanolic HCl)	0.10 (lower)
	0.33 (upper)
Erythropterin	0.10 (lower)
	0.33 (upper)
<i>Colaenis</i> pigment (extracted with methanol)	0.53
Rhizopterine	0.49
Xanthopterine	0.39

pterine is as yet undetermined. Both its UV and visible spectra are quite similar to those of the erythropterine and the *H. erato* extract. However, relative intensities of the individual peaks



TEXT-FIG. III. Ultra violet-visible spectra of the erythropterin sample dissolved in methanol. Refer to Table I for numerical data and for acid-base additions.

are quite different. Also, the R_f of this particular pterin is 0.55 as opposed to 0.10 and 0.33 for the erythropterin forms. Chromatographic and spectrophotometric comparisons with samples of rhizopterin and xanthopterin yielded dissimilar results.

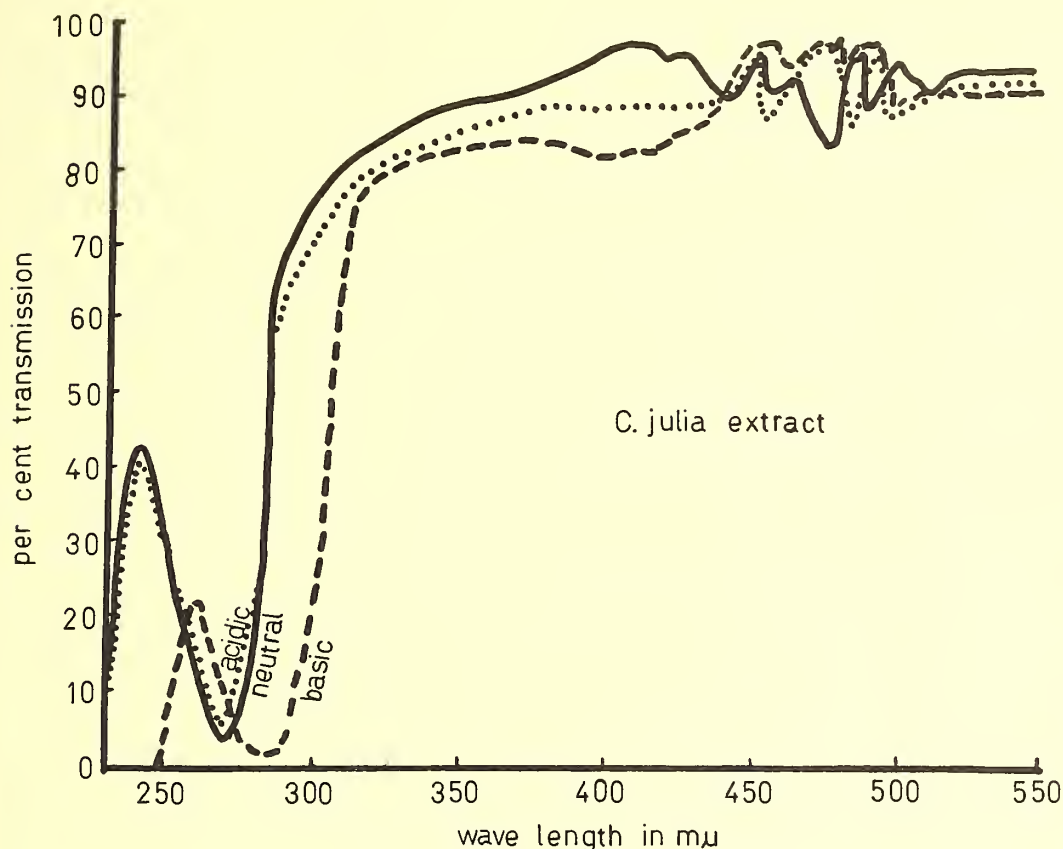
Heliconius sara, a black Heliconiid with two yellow bands on each forewing, was also examined. Its yellow pigment is known to be a new L- α -amino acid (Brown, 1965). However, it was checked in order to determine whether or not a pterin was also contributing to the yellow color. The resulting data were quite dissimilar to those obtained from the *H. erato* or *C. julia* specimens. The chromatographic and spectrophotometric data were identical to those of Brown and no indication of a pterin was found.

CONCLUSION

From the above data it can be concluded that erythropterin exists as a pigment within at least

one Heliconiid butterfly. Also, there is no reason to doubt that it exists in other members of the same family since many have the same distinct red coloration on various portions of the body. The pigment is no doubt located on the walls of canals in the scales as it is in pierid butterflies (Ziegler-Günder, 1955).

The spectrum of the pigment extract is identical with that of the erythropterin. The fact that two spots appear on chromatograms both with the erythropterin and the methanolic HCl extract seem to indicate that this is probably not the case. There is good indication that an equilibrium exists between the two forms of this pigment. Tschesche & Barkmeier (1955) and Fieser & Fieser (1963) have suggested that erythropterin may exist in equilibrium with a tricyclic form (Text-fig. I). Excellent support for such an equilibrium is found in the fact that when individual chromatogram spots were eluted and re-run, two spots were again obtained. Both had the same R_f values and the same fluor-



TEXT-FIG. IV. Ultra violet-visible spectra of the pigment extracted from *Colaenis julia* with methanol.

escence as did the original sample. A second and less likely explanation is related to the relatively unstable nature of pterins. It might be possible to assume that certain changes in or the loss of portions of a side chain or group might cause a change in R_f without a corresponding effect upon the UV spectra (Nawa, Goto, *et al.*, 1964).

When comparing the visible spectra of Text-figures II and III, it is obvious that a discrepancy exists in regard to one of the principle peaks (480 $m\mu$). When the neutral *H. erato* pigment is made alkaline, the 480 peak shifts out but returns upon acidification as expected. The erythropterin, however, does not do this. The 480 peak shifts out with the addition of alkali but fails to return upon acidification. This is attributed to the fact that approximately equal quantities of acid were added to the solutions of erythropterin and pigment extract. It was later realized that excess acid was needed to cause a complete re-shift.

An unidentified pterin has been detected in the orange wings of *Colaenis julia*. It possesses all the properties of pterins, has a spectra similar in shape but not intensity to that of erythropterin but has a different R_f .

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3

Underwater Sound Production by Captive California Sea Lions, *Zalophus californianus*

RONALD J. SCHUSTERMAN
ROGER GENTRY
&
JAMES SCHMOOK

Stanford Research Institute
Menlo Park, California

(Plates I-V)

INTRODUCTION

THUS far, it has been shown that the California sea lion, *Zalophus californianus*, produces two types of underwater sounds—clicks, or short-duration sound pulses, and barks (Poulter, 1963; Schevill, Watkins & Ray, 1963). In contrast, the bottlenose porpoise produces a wide variety of sounds—clicks, whistles or squeals, barks (Evans & Prescott, 1962), and “cracks” (Caldwell, Haugen & Caldwell, 1962). Although the clicks are used for echolocation by the porpoise (Kellogg, 1961; Norris, 1964), there is evidence indicating that a variety of whistles have emotional and communicative significance. Some whistle contours and the crackling sounds have been said to be associated with distress or fright reactions (Caldwell *et al.*, 1962; Lilly, 1962).

Underwater clicks by *Zalophus* have been reported to occur usually when an animal was in the final stages of searching for food (Poulter, 1963; Schevill *et al.*, 1963) or for an object signalling food (Evans & Haugen, 1963; Schusterman, 1966). Most of these tests have limited the range of behavior to those involved in feeding activities. In order to determine whether *Zalophus* is capable of emitting a greater variety of underwater signals and calls than had been previously reported, several California sea lions were monitored while swimming freely under a number of stimulus conditions.

PROCEDURE AND APPARATUS

All observations and recordings were made while animals were swimming untethered in an oval tank constructed of redwood, measuring 15 feet by 30 feet and 6 feet deep, and filled with 82 kiloliters of fresh water. Recordings of the underwater sound productions by *Zalophus* were made under the following conditions: (a) conspecific social interaction; (b) orientation to a mirror; (c) fleeing from a human observer.

Underwater sounds were continuously monitored by a Channel Industries 275 hydrophone (20 Hz to 150 kHz) and an Ampex 2044 amplifier-speaker system (65 Hz to 13 kHz). Vocal signals were periodically recorded on a Uher 4000-S tape recorder at 7.5 inches/second (40 Hz to 20 kHz).

Spectrographs of the evoked signals were made, using the Kay 661 sonograph. Either of two analyzing bandpass filters (narrow or wide) may be used with the Kay sonograph. The wide-band filter has an effective bandwidth of 300 cycles, and the narrow-band filter has an effective bandwidth of 45 cycles. The analysis used is indicated on each of the spectrographs presented. The use of this method for the analysis of biological sounds has been described by Borror (1960).

RECORDED SOUNDS

Clicks.—Our preliminary analysis indicates

that *Zalophus* produces a great variety of click patterns. Although most of the click trains have a duration of 2 seconds or less, many trains last as long as 23 seconds with pauses of less than 0.5 second. The click repetition rate may vary from less than 5 per second to 70 or 80 per second, all within a given click train (separation between clicks of 0.5 second or less).

Plate I is a spectrograph of clicks produced by one sea lion while play-fighting with another sea lion. When the tape which produced this spectrograph was replayed, we noted that a popping sound seemed to be superimposed on the clicks. This is indicated on the graph, we believe, by the great variation in the frequency pattern. Such a sound pattern is highly distinctive and has been produced by only one of the animals (Cathy).

It is important to note that clicking sounds were never emitted at fairly regular intervals by any of the animals under any of the free-swimming conditions. This is in marked contrast to the behavior of the bottlenose dolphin, which is reported to emit "exploratory" pings every 15 to 20 seconds. Such periodic signal emission has been suggested as the sonar equivalent to "glancing" in the field of vision (Kellogg, 1961).

Barks.—This form of underwater vocalization has most of its energy below 3500 Hz, although some energy may be found at frequencies as high as 8000 Hz. There is little variation in the duration of any given bark; they generally last from 200 to 300 milliseconds. Barks are sometimes preceded by a series of clicks, as shown in Plate II. The sounds shown in this plate were produced by a two-year-old male *Zalophus* while it was fleeing from the experimenter, who was attempting to drive the animal out of the testing tank. During the experimenter's initial attempts, the animal swam rather rapidly while producing long trains of clicks. As the action became more intense, the clicks shifted into a series of barks.

Whinny.—A spectrograph of this vocalization is shown in Plate III. It was frequently produced by a 3.5-year-old female *Zalophus* (Bibi) during an aggressive encounter. For lack of a better term, we have called it the "whinny" sound, since it sounds a little like a horse neighing. This vocalization is often preceded by clicks or a growl sound. The whinny sound typically lasts for about 1.5 seconds and may be repeated three or four times in succession. This whinny sound may be the female counterpart of a male bark. However, contrary to another report (Bonnott, 1951), we have heard females bark both in air and submerged.

Buzzing.—A characteristic "buzz" sound from a sea lion in a social situation is depicted in

Plate IV. This vocalization may actually be a series of discrete sound pulses which occur so rapidly that they take on a buzzing quality.

Bang or Crack.—This sound has thus far been produced by two of our California sea lions (a male and female). The sound was first heard when Bibi was confronted with its mirror image and was repeated several times over a period of days, usually under the same circumstances. Plate V shows a pair of these high-energy "bang" sounds. The sound, which has always been associated with extremely rapid swimming, appears quite loud and mechanical to the human ear, and, as the spectrograph shows, it is a broadband pulse with a rapid onset. Apparently, from the description of Caldwell *et al.* (1962), *Zalophus*' "bang" sound is very similar to high-energy "crack" sounds produced by *Tursiops truncatus* under conditions of fright. We have recently heard similar sounds produced by Steller's sea lion (*Eumetopias jubatus*) while performing on an underwater visual discrimination task.

SOUND PRODUCTION MECHANISMS

Careful observations of *Zalophus* while it was in the act of emitting underwater clicks have indicated some movement in the area of the throat or larynx; such movement appeared less pronounced when the animal was silent. These preliminary observations implicating the laryngeal area as the underwater sound-producing site of *Zalophus* have been supported by experimental evidence (T. C. Poulter, 1965). Using a triangulation technique, Poulter found that the site of underwater barking was the vocal cords on the anterior portion of the larynx and that the apparent point of origin of underwater clicks was posterior to the vocal cords.

All of the underwater vocalizations that have been described can apparently be produced with the mouth and nostrils closed and therefore without the emission of bubbles, or with the mouth and nostrils partially opened and with the emission of bubbles. Moreover, clicks may be produced in air with the mouth closed or with the mouth wide open. Barking sounds seem to show the same basic frequency-intensity structure in air and under water. However, clicking in air is usually less intense and much less frequent than under water. Although no systematic attempt has yet been made to measure the intensity of *Zalophus*' underwater clicks, there has been no difficulty in monitoring these sounds even when the background noise was considerable and the animal was as far as 5 to 6 meters from the hydrophone.

It is not clear how the "bang" sound of *Zalo-*

phus is produced, i.e., whether it is made by the sea lion's vocal apparatus, by jaw-clapping, or by some other mechanism such as the front flippers causing an underwater cavitation as they are thrust together and then parted during initiation of a very rapid swim.

DISCUSSION

Thus far, all of the underwater sounds produced by captive California sea lions have had a pulsed structure and appear to be wholly or partly a function of social or investigatory responsiveness. The shifting from clicking to barking or to a whinny sound under conditions of either extra-specific or conspecific intimidation suggests that these calls form a single system of vocalization which changes as a function of the level of physiological arousal (Duffy, 1957), with barking indicative of a higher level of arousal than clicking. This notion is similar to that held by Andrew (1962, 1964), who has developed the concept of "stimulus contrast" to account for the vocalization of chicks and non-human primates.

Although there are certain similarities between the sonar signals of the porpoise (*Tursiops truncatus*) and the clicks of *Zalophus californianus*, there are also great differences. Whereas the clicks of the porpoise are very narrow columns of "noise" having their greatest energy up to 30 kHz, with components of lesser intensity reaching 170 kHz (Kellogg, 1961; Norris, 1964), those sampled from *Zalophus* thus far often contain at least traces of harmonics and have their greatest energy at 500 Hz to 4000 Hz, with possibly weak components extending to higher frequencies. Furthermore, regarding the porpoise, Norris reports that "during fine discriminations where sight is impossible, the environment is literally saturated with tiny plosive clicks, up to 500-600 per second," (Norris, 1964, p. 320). Such rapid pulsing has not been consistently produced by *Zalophus*.

SUMMARY

Spectrographs are presented of underwater sounds made by captive sea lions (*Zalophus californianus*) under the following conditions: (a) social interaction; (b) orientation to a mirror, and (c) fleeing from the experimenter. These animals produce a variety of vocal utterances and sounds, including varying patterns of clicks, barks, "whinny" sounds, "bangs," and buzzes. All sounds thus far recorded and analyzed have a pulsed structure with dominant frequencies ranging from 500 Hz to 4 kHz. The sounds appear to be wholly or partly a function of the

social and investigatory responsiveness of the sea lion.

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EXPLANATIONS OF PLATES

PLATE I.

Spectrograph of clicks emitted by a 3-year-old female California sea lion (Cathy) while play-fighting with another sea lion (narrow band).

PLATE II.

Spectrograph of clicks and barks produced by a 2-year-old male (Tommy) while fleeing from the experimenter (wide band).

PLATE III.

Spectrograph of Bibi's "whinny" vocalization pro-

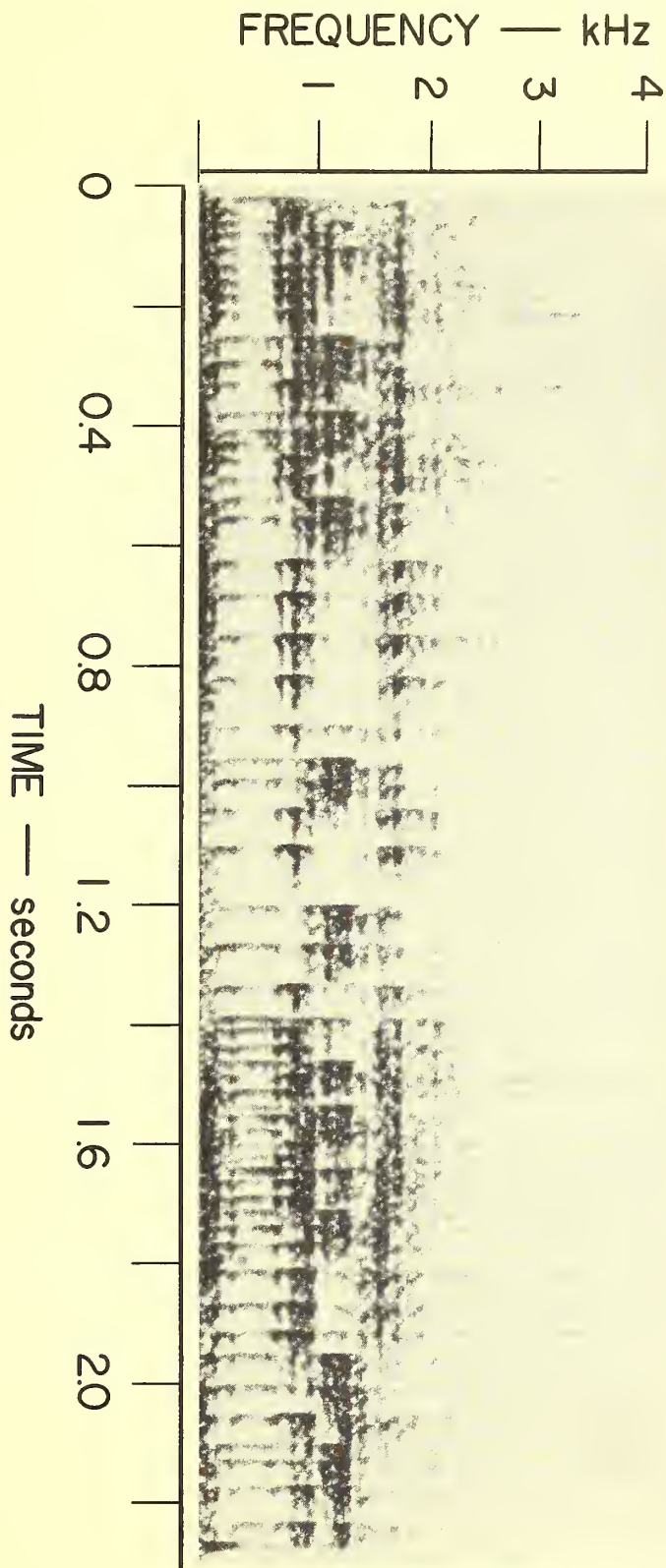
duced during an aggressive encounter with another California sea lion (narrow band).

PLATE IV.

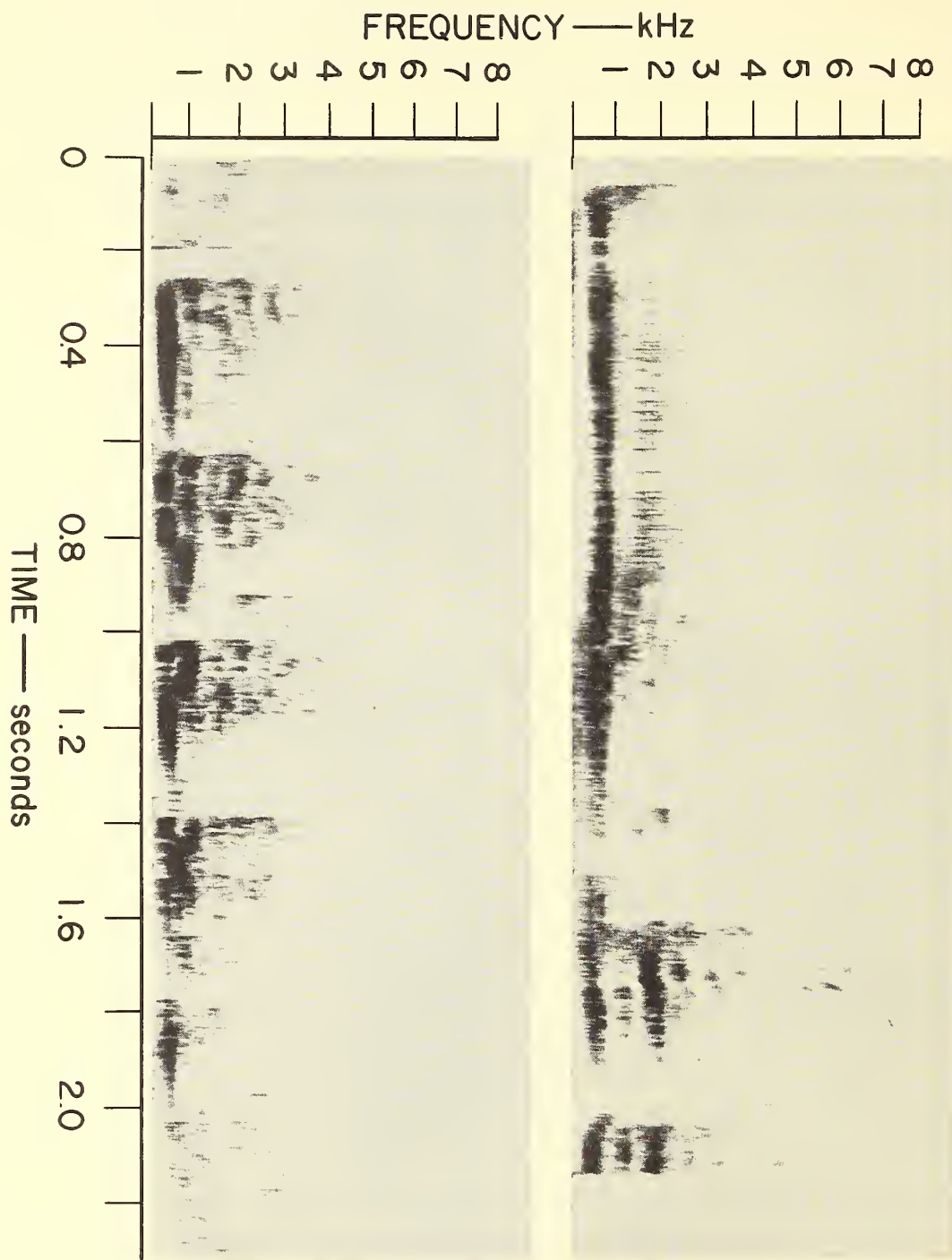
Spectrograph of a "buzzing" sound emitted by Cathy while swimming with another California sea lion (narrow band).

PLATE V.

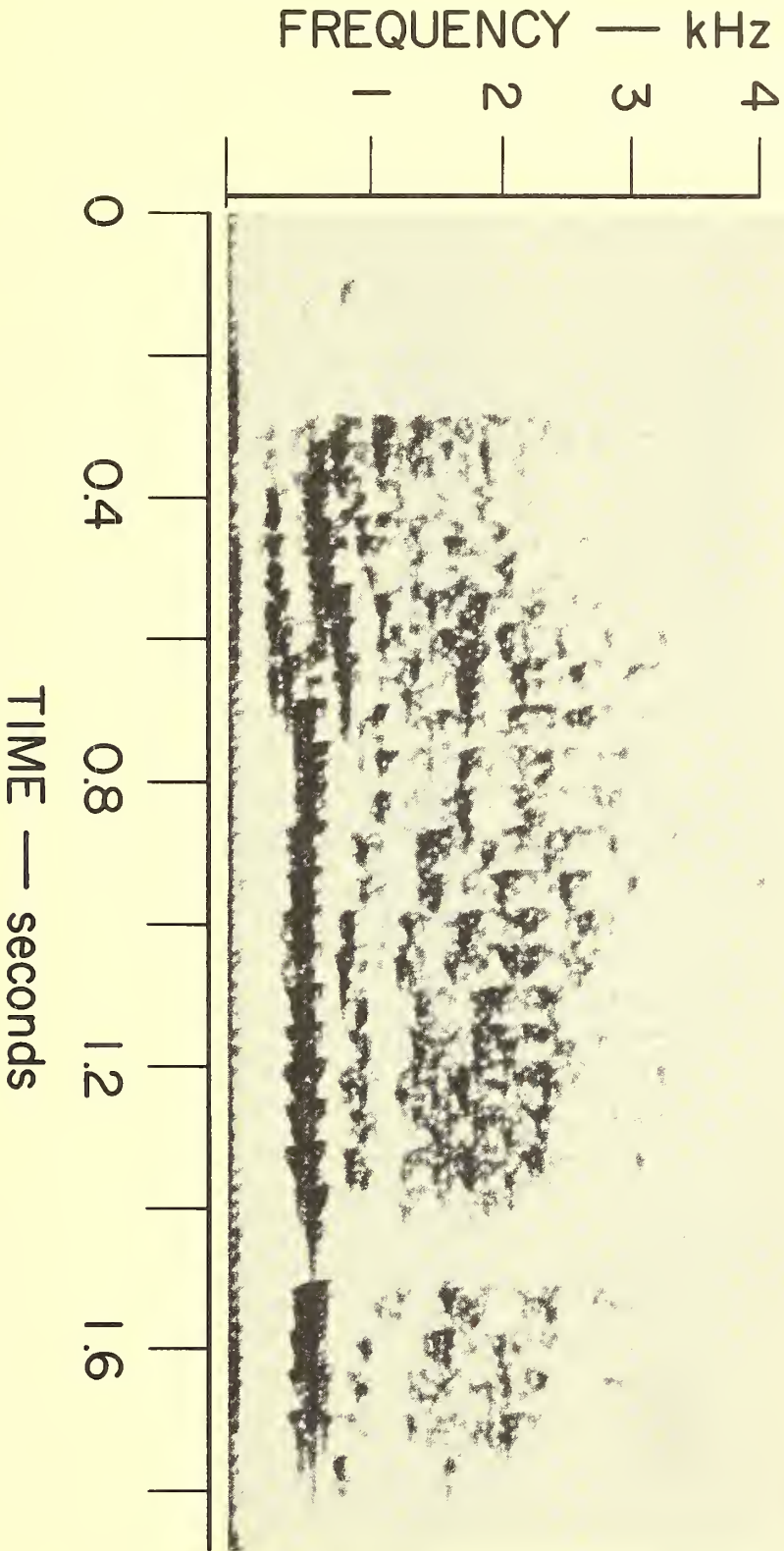
Spectrograph of two "bang" sounds produced by a 3-year-old California sea lion (Bibi) while orienting to a submerged mirror.



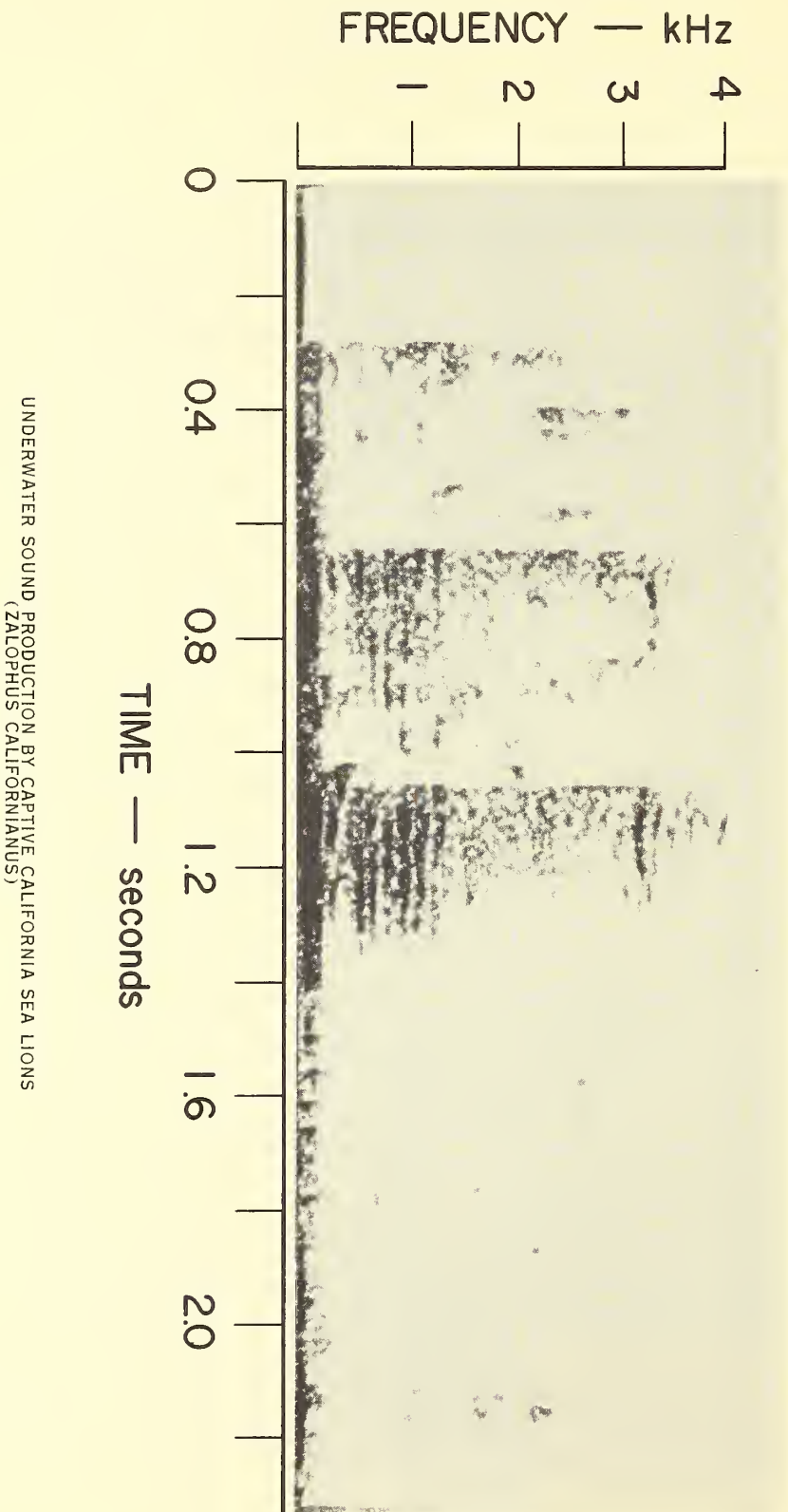
UNDERWATER SOUND PRODUCTION BY CAPTIVE CALIFORNIA SEA LIONS
(ZALOPHUS CALIFORNIANUS)

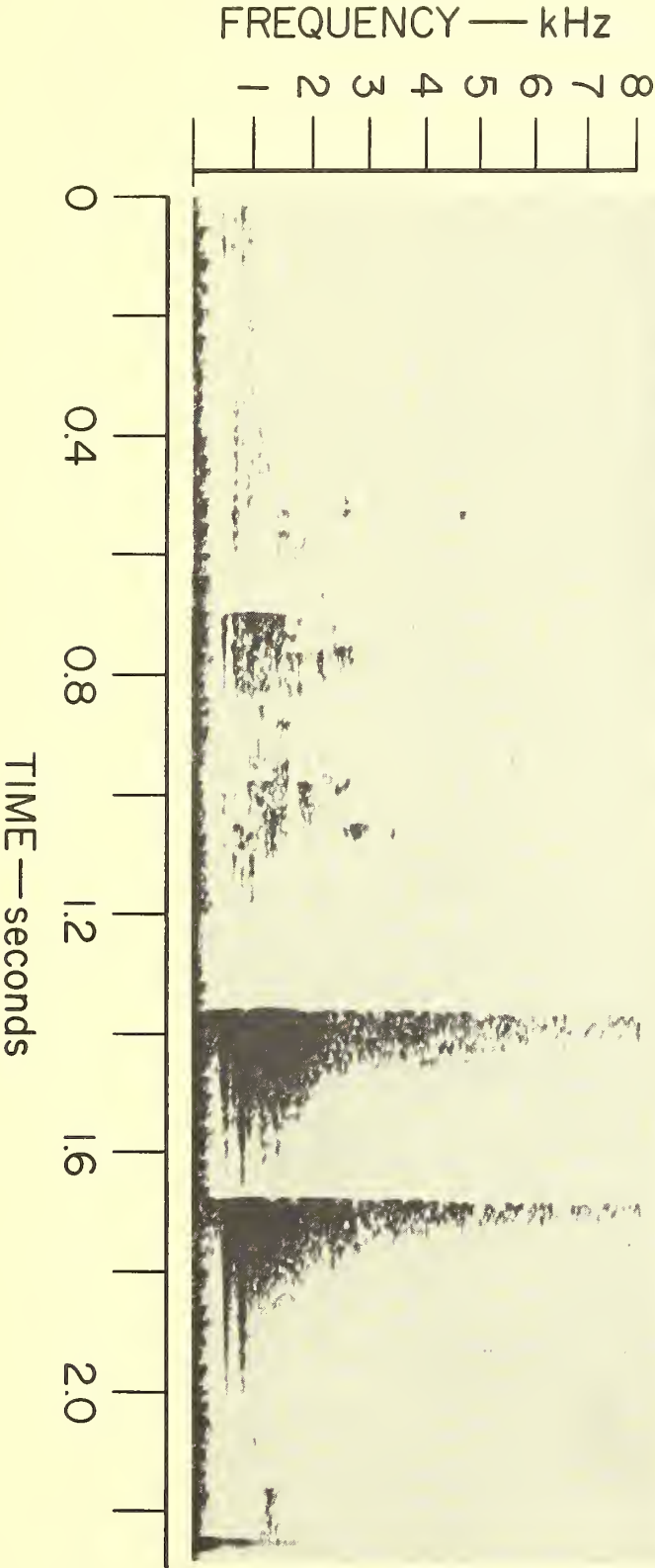


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UNDERWATER SOUND PRODUCTION BY CAPTIVE CALIFORNIA SEA LIONS
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On the Survival Value of Fish Schools

C. M. BREDER, JR.

The American Museum of Natural History

and

Cape Haze Marine Laboratory

INTRODUCTION

THE QUESTION of whether the typical schools or other groupings of fishes have survival value has often been raised, but few investigators have gone into the matter in any depth. One approach, which might be called the anecdotal or the naturalist's approach, is usually given as a general verbal interpretation, based on simple observation. Another, which might be called the mathematician's approach, is typically given as a rigorous analysis of a schematic abstraction of a fish school, usually as an oversimplification, in which prey and predators are considered as making more or fewer encounters, based primarily on random movements. The first may be exemplified by Breder and Halpern (1946), Hiatt and Brock (1948), Sette (1950), Springer (1957), Milanovskii and Rekubratskii (1960) and von Wahlert (1963). The second may be illustrated by Brock and Riffenburgh (1960) and Olson (1964). There is, of course, merit in both these approaches, but neither, by itself, would seem to be adequate to develop a full understanding of the phenomenon. A third approach would, of course, be the experimental one, but there have been only two reports directed toward the possible significance of schools to survival (Williams, 1964; John, 1964). The recent great activity in the study of schooling, on aspects other than possible survival value, has nonetheless useful data to contribute to this subject.

The primary purpose of the present paper is to indicate clearly that all fish schools are not necessarily similar structures, nor that they could be encompassed in a single formulation. A considerable amount of material has been examined and various theoretical considerations

have been drawn into the present study. This treatment makes it possible to show, at least at minimum, some of the complications necessarily involved in any attempt to assign a specific survival value to a given fish school under definite conditions of existence.

Valuable assistance has been freely given by Dr. Eugenie Clark on matters concerning visibility and certain aspects of assemblage and by Dr. William N. Tavolga on features of underwater sound and its consequences. The complete manuscript has been critically examined by Dr. James W. Atz. Drs. Donn E. Rosen and W. N. Tavolga examined those sections in detail pertinent to their interests. To these people the author is grateful for the help rendered.

DEFINITIONS

As in most fields that are undergoing rapid growth there is considerable variety in the usage of words and terminology. This is a normal symptom of an active and changing field. It is brought about primarily by differences in the interests and purposes of the earlier writers on the subject. Evidently there are still too many new facts and ideas developing to expect an early stabilization or general agreement on usage. Thus it behooves all workers in the area to indicate scrupulously just how they are using any terms that could possibly lead to confusion and misunderstanding. Also readers should use great care to be sure that they understand an author's precise meaning. In addition to definitions in this section, differences in point of view and usage are indicated wherever clarification would seem needed.

The word "school" has a long history of common usage in connection with fishes and many

dictionaries give as a definition, "a large number of fish swimming together," or some equivalent. The connotation would ordinarily be that if they were swimming together they would be going in the same direction, as opposed to churning about or simply resting. Parr (1927), Atz (1953) and Breder (1929 through 1965) have used the word essentially in the sense of the ordinary dictionary definition. Spooner (1931) attempted to restrict the use of "school" to cover only social groups, as opposed to groups drawn to one place by non-social influences. Certainly there is no objection to redefining a word for technical purposes when such a modification of usage is justified. However, it is seldom possible to determine what motivations are effective in the formation of a school. In most cases it is difficult or impossible to define what determines the formation of any type of fish group. There is always at least a residue of both a social and non-social influence present for the fishes must at least tolerate each other and must be located where they are because of non-social influences, such as temperature, nearness to surface or bottom, light, *et cetera*.

It is partly for the above reasons that the more nearly objective and always recognizable measure, not concerned with what drives the fish may or may not have, has been used here. Williams (1964) objects to this usage stating, "It may be of some value to distinguish these two phases of activity,¹ but the difference between social and non-social groupings is in greater need of terminological distinction." This, of course, is a measure of the difference between two approaches, needs and purposes. It very nicely illustrates the point made in the preceding comments. The field is still in such an uncongealed state that it is possible for two very thoughtful papers (Brock and Riffenburgh, 1960; Williams, 1964) to express essentially opposite points of view.

Milanovskii and Rekrubratskii (1960) who consider "... schooling behavior as one of the adaptive features of a population of a single species ..." use the word "school" in an even broader way than does Williams and indicate that the usages of Parr, Keenleyside (1955) and others are "one-sided" and "contain mechanistic elements." At least there is agreement in the present paper with their comment, "At any stage of elaboration of the problem we find it necessary to have a working hypothesis—tentative definitions of school and schooling behavior, which should be based on the present level of

our knowledge."

Williams (1964) develops the idea that schooling and aggregating are basically rooted in a tendency to hide behind something, as a response to "fright." He carried out experiments bearing on this idea, with a number of species of essentially aggregating types of fishes, as did John (1964) on *Astyanax*. Both found that in a "blank" environment their fishes tended to stay together and formed aggregations or "fright schools." With these experiments there is no disagreement, but an examination of them may help to further clarify the different usages and attitudes toward the word "school." If the correspondingly opposite experiments be made of placing permanently-schooling fishes in an environment of abundant and varied cover these fishes will not hide behind anything, even if completely isolated from others of their kind. They merely go into a period of fast and erratic swimming, evidently in search of companions—behavior that looks surprisingly like "panic." It is not uncommon for them to exhaust themselves, collapse and promptly expire. For this reason the term "obligate schoolers" would seem to be appropriate in contrast to fish that may be called "facultative schoolers." Under such conditions of isolation, obligate schoolers will attempt to school with practically any fish, solitary or not, that may be presented. These may be very unlike, for example, *Mugil* "schooling" with *Canthigaster* (Breder, 1949). Evidently it is the motion of another swimming fish that induces the otherwise isolated obligate schooler to react, while they do not respond at all to inert objects. Formal experiments hardly seem necessary in this connection, as the action seems to be entirely evident. The attempt to experiment with these extreme types is, in any case, difficult. They are notoriously difficult to even establish and keep in aquaria. This is the principal reason why scombriform, carangiform or clupeiform species are seldom seen on display in public aquaria.

Williams performed his experiments on *Anguilla rostrata* (LeSueur), *Hyphesobrycon flammeus* Myers, *Notopis antherinoides* Rafinesque, *N. stramineus* (Cope), *Pimephales notatus* (Rafinesque), *Xiphophorus* hybrids, *Poecilia reticulata* Peters, *Lepomis cyanellus* Rafinesque and *Colisa lalia* (Hamilton-Buchanan).² Not

¹ That is, "schooling" and "aggregating" in the sense used here. This footnote mine.

² Breder and Halpern (1946) and Breder and Roemhild (1947) performed somewhat related experiments in which they analyzed the statistical deployment of a number of similar species of fishes, none of which were obligate schoolers. All such work on aggregating forms, while useful, is not adequate to determine the behavior of obligate schoolers.

one of these is an obligate schooler. They may form aggregations in the non-polarized sense, fright schools, schools in rapidly-flowing water or other facultative assemblages. If this was all there was to the matter no one would have thought to differentiate chronic schoolers from the others. It is here that the confusion about this term and its usage arises. In an attempt to clarify the present point of view, the following details are brought together to enable a perhaps clearer separation of the obligate from the facultative.

To be considered obligate, schoolers must be coherently polarized; can only be forced to stop schooling momentarily, and then only by means of considerable violence; and will not maintain a state of random orientation. The group is permanent, excepting only when physical conditions in the environment suppress the functioning of some essential system, usually the optical, as on an extraordinarily dark night. Isolated members display erratic locomotion and commonly cannot exist for long in the solitary state. The drive to associate with others in a body of great unanimity of orientation is clearly a positive matter of great strength, quite unlike the fragile schools of fright, or other temporary mutual orientations seen in fishes which otherwise are found more commonly in non-polarized aggregations or as solitary individuals. For fully evident mechanical reasons only schooling fishes are able to form fish mills, a type of circular swimming which occurs regularly in obligate schools. The non-polarized aggregations are fully unable to form the mill structure. See Breder (1965) for an extended discussion of this phenomenon.

In the terminology proposed by Williams, "school" refers to any group of fishes "... that owes its persistence to social (but not sexual) forces" and "aggregation" refers to "... groups that arise by individuals independently seeking the same localized conditions", which is in agreement with Spooner (1931). Probably all groups contain an element of both "school" and "aggregation" in the above usage, except the obligate schoolers, as here used. That is, the obligate schooler is so locked to its fellows that it ignores other things in its environment to a remarkable extent while the facultative schooler clearly is more actively involved with other environmental details, often ignoring his fellows to the point of losing its group altogether. Of this Williams was aware when he wrote that "... when one observes a dense con-

centration of the same species moving about in a pelagic or other uniform habitat . . . he is probably safe in calling it a school . . .," but that "schools and aggregations cannot be as confidently distinguished in heterogeneous environments, and it must often happen that groups are formed that owe their cohesiveness to both schooling and aggregation in mutual reinforcement (heterogeneous summation of Tinbergen, 1951)."

Thus it appears that what would seem to be two very different positions are not as far apart as might be thought for, in many cases, if not all, by designating species by either system a very similar listing would develop. That is to say, what are designated as schools in the present view are assembled on a great preponderance of social tendencies, while aggregations are assembled with a far greater content of general environmental influence. This is precisely the view propounded by Williams, and in an area where so little is yet known, may be very useful as a first approximation on what holds the group together, that is, primarily social influences or non-social influences.

ANALYSIS OF PERTINENT DETAILS

The treatment of the available data in this section has been broken down into several subsections, bringing together the controlling influences of the environment and their effects under various conditions of predation.

THE INFLUENCE OF ENVIRONMENT

A suitable point of departure is a consideration of the sensory modalities that are dominant in schooling fishes and the effects of various environmental influences on their functioning.

Visibility and transparency of water

It has been abundantly shown that vision is necessary for the formation and maintenance of fish schools, see for instance, Parr (1927), Atz (1953), Breder, (1959), and Blaxter and Parrish (1965). Also, blind fish and fish in total darkness are unable to maintain this highly polarized arrangement. Obviously the transparency of the water is of great importance to any behavior so largely dependent on vision. This was clearly recognized by Brock and Rifenburgh (1960), in connection with vision's role in school maintenance, when they wrote, "A consideration of the optical peculiarities of water is pertinent in this connection. The distance an object of given size can be seen depends upon two factors: the intercept angle at the eye and the contrast difference between the

object and the background. Due to backscatter and light absorption an object of high contrast will fade from sight regardless of size at a relatively small distance, say 200 feet or less, even in the clearest water. This means that for objects above a fairly moderate size, large enough to give an intercept angle adequate for effective vision at the distance where light absorption and backscatter reduce contrast difference to a point of invisibility, taken at 2 per cent, for man (Duntley, 1952), any increase in size of the object will not effectively increase the distance at which it may be seen. The critical intercept angle for the human eye is taken to be one minute which would occur for an object 0.72 inches in diameter at 200 feet." This obviously gives a measure of the extreme visibility range under water, which in most places is not even closely approached. It may be that this estimate, although based on Duntley's paper, is too high, for he, in another place, wrote, "It is expected that water having hydrological range³ as great as 130 feet will be found in the Sargasso Sea and in the Mediterranean." In a personal communication, Dr. Eugenie Clark estimated that horizontal visibility as great as 180 feet occurred off the Caribbean coast of Yucatan.

Before distances as great as those mentioned above are brought into the discussion, there are considerations involving the geometry of fish schools operating completely within the area of full visibility, which can properly be discussed at this point. Since fish often tend to accumulate into "balls," see for instance Breder (1959), they thereby also tend to occupy the minimum space and show the least surface area. This is also done by a droplet of fluid for purely mechanical and geometrical reasons. The result is to incidentally produce a figure of least conspicuousness and therefore to possess some presumed selective value. This we might call "primary selective value," in which the *direct* response to a stimulus, which may be a simple physical condition, produces a result of definite selective value. Viewed this way, it follows that departure from the spherical form may be taken as a measure of the extent to which other influences make the fishes independent of this or

other similar constraints. In its place come other constraints, which may be thought of as "secondary survival values." These are, of course, the types of selective activity ordinarily referred to as simply "selective values," by evolutionists. When the primary and secondary selective processes both press in the same direction, it is often difficult, if not impossible, to clearly separate them, but it is here that one would expect the development of great stability of behavior or structure or whatever the selective processes have been directing. Anyone familiar with schooling fishes can attest to the strength and rigidity of the habit. Departures from it are clearly associated with special circumstances. Some of these may be considered merely various deformations of a primary tendency toward a globular school, or even a non-polarized aggregation, for in this feature both schools and aggregations show similar tendencies.

Deformations may be related to groups forming close to the water surface and spreading out like a rising globule of very viscous oil. A similar case, on the bottom, would be like a globule of heavy oil spreading out. In very shallow water both surface and bottom would exert deformative influences. Also elongate schools are normally associated with fish migrating or under other kinds of highly directional travel.

As a more generalized concept of the geometry of schools, their size and the restrictions of lateral visibility in water, the following situation may be postulated. Given a case where a single individual, prey or predator has a useful visual range of, say, 30 feet, each solitary individual fish may be considered at the center of a sphere with a 30-foot radius. This is too much of an oversimplification, however, for the restrictions on vision from above and below are somewhat less than in any horizontal direction. In the case of looking down, an object below is more fully illuminated than any side view of one at the same depth. In the case of looking up, the fish is silhouetted against the illumination from above. The resultant increase of visibility, both up and down, increases the visual range vertically to an extent determined by turbidity, light angle, *et cetera*, except for the following facts. These differences in visibility, owing to direction, are the precise ones that are minimized by countershading. In most clear open waters countershading is notably efficient. Consequently it is more nearly correct to think of an individual fish as at the center of a geometric figure approximating a very slightly prolate ellipsoid with its long axis vertical and the horizontal axis, coinciding with that of the fish, longer than the transverse axis.

³ Duntley (1952) defined "hydrological range" as follows. "The clarity of water can usefully be specified in terms of *hydrological range* (v). This is the distance measured along the path of sight, at which the apparent contrast of any object seen against a deep water background is reduced to two per cent of its inherent value. Along a horizontal path of sight hydrological range (v_0) is related to the transmittance (T) of the water (as measured by a hydrophotometer) by the equation

$$T = e^{-3.912x/v_0} \quad (4.1)$$

where x is the distance from the object to the observer." For the derivation of this expression see the original.

As a matter of simple geometry, several propositions follow. One fish or a "school" of two has practically the same lateral range of vision and there is little increase in the ability of two fish, forming a "school," to detect a predator, over the ability of a single fish. This is because the "inner side" of each is either blocked by its companion or, if not, their fields of view are almost completely duplicative. As a school increases in the number of fishes the range of vision increases proportionately to the area of the side presented. As both prey and predators wander about, there is thus twice the chance of an encounter with two single fish, not encroaching on each other's field of vision, as with two fish together in a school.

The above is precisely calculable and is independent of concerns of Duntley (1952) so long as the fishes do not wander beyond their mutual visibility ranges. Examples cover only certain fishes indigenous to very shallow water, or living near the surface where illumination is not notably attenuated. Here small fishes such as *Jenkinsia* or *Sardinella* are often preyed upon by immature carangids and *Sphyræna* or mature *Strongylura*. The schools may be large, up to over a thousand or more individuals, with the predators cruising about with the prey in full view. The predators may be typically solitary (*Sphyræna*) or in small bands themselves (*Strongylura* and *Caranx*). Any of them may strike into a school and pick off their prey at will, either alone or as two, or rarely a few, actively-feeding predators. In the above named fishes, multiple attacks are most common in the carangids. Presumably the predators under such situations are generally filled to satiation. Field observations have shown that individuals coming in from some distant point beyond the range of visibility, and new to the school of prey, usually pick off a few fish and then rest idly nearby. From then on it is only occasionally that one will dash in to take a single fish, with extended idle intervals between. The length of these intervals is presumably a measure of the degree of digestive satiation which an individual predator has reached. The situation above described is one that can be generally found in regions where such fishes abound and is apparently the normal circumstances under which they usually exist. This could be conceived of as the degenerate limit of the situations involving no limitation on visibility, as earlier discussed. Here the predators are never under prolonged hunger and escape of a school unscathed never occurs. Also here the maintenance of a population of prey species must depend more on reproductive potential or continued recruit-

ment from "safer" environments, with little or no dependence on locomotor activity for escape in flight. However, even within the limits defined, the least healthy, alert or most awkward, would on the average, be systematically eliminated. From the standpoint of selection theory, this in itself could be valuable to the long-time survival of the population.

Sound production and its prevention

The problem of sound production by the swimming efforts of schooling fishes or their predators is presently unclear for several reasons, see for instance Winn (1964), Wodinsky and Tavalga (1964) and van Bergeijk (1964). Ordinarily most fishes make no appreciable sound incident to their locomotor activity but may do so on sharp turns, see Moulton (1960). His observations check well with our own in this respect, considering that different fishes were under sonic observation. Very little on swimming sounds has been reported by acoustical students on either individual fishes or fish schools. This is most notable in observations made in light. It is possible that there has been selection tending to reduce activities and structures responsible for the production of sounds. If this is the case, then schooling fishes that are reported to produce sounds in the dark, see for instance Takarev (1958), Shishkova (1958), Moulton (1960) and Marshall (1962), could represent an overriding nocturnal specialization toward the prevention of too-wide dispersal under lightless conditions. To predators with sonar echo mechanisms, such as porpoises, fish sounds or their absence would apparently make little difference, if any. These forms are able to feed by locating fishes by means of their echo-ranging mechanisms alone, the data on which is summarized by Norris (1964).

The above should not be interpreted to mean that a complete silence is present in a school of fishes, but only that its magnitude is too small to be effective at distances under which predators have to operate. The sounds noted by Moulton (1960) when sharp turns are made by fish schools are evidently only produced under some fright-inducing stimulus. This means only that fish already sensing the near presence of a predator in their locomotor escape efforts, exceed some physical limit above which higher sound levels are reached. This occurs at a time when quietude is evidently no longer as important as flight.

Tavalga, in a personal communication, wrote as follows about the quality of sounds produced by a "smoothly" moving school, "The quality of this noise is interesting in that it would tend

to be random since all the fish-tail movements are not perfectly in phase. Such a noise might tend to be masked by ambient noise. Therefore, even if a predator might be in the range of this school noise, he might perceive it as only a slight increase in ambient noise level, as might be produced by wave action or some other physical phenomenon." These sounds would, of course, be quite different from the various nighttime sounds described by authors, often as clicks or taps, and which are clearly not sounds made incidental to locomotion.

A point to be considered about the above is related to the information provided by the sonar instruments such as those used by anglers to locate fishes. These devices, because of the Doppler effect, provide not only an indication of the presence and species but also an estimate of the size of the fish or fishes and the numbers present. This information is based on the pulsations provided by the motion of swimming fishes, which are characteristic for most species and sizes. Of course, the reflected high frequencies used by these instruments, brought down to the audible range by electronic means, are not identical with the low frequency, faint sounds produced by the fishes themselves. However, if these are audible at all, they must have a beat basically similar to that of the ultra-sonic reflected frequencies. It is certainly true that many schools are so lacking in swimming synchronization that only a broad band of low frequency noise could be expected. However, schools vary from those in which the individuals are completely out of phase to those that have well over 50 per cent of the members in good swimming synchronization. Occasionally small schools, usually of not more than a dozen individuals as seen in various species of *Mugil*, *Caranx* and a variety of scombrids, are clearly in near perfect phase. Schools, other than the ones lacking any substantial synchronization, would introduce a type of "noise" containing a beat, more or less masked, but which should be able to convey information to a predator, including estimates of species, size, number and direction of travel. These thoughts introduce an unexplored area, including the extent of synchronization in fish schools, the reasons for its presence or absence and a study of its sonic product, including volume and characteristic beat. All this should be amenable to an instrumental approach. Indeed the schools without individuals in phase may be an adaptation to the need for the suppression of telltale sounds rather than the other way around.

Bearing on this is the question of the ability of fishes to detect the direction from which a

sound emanates. It has been argued by Harris and van Bergeijk (1962), van Bergeijk (1964) and Harris (1964) that far-field effects are virtually non-directional for fishes, while near-field effects are highly directional. Thus, a school out of visual range and beyond the near-field might not give a predator sonic cues as to its location, but nonetheless, the sounds might stimulate intensified ranging activities on the part of the predator that could lead the latter to its target on a basis of increasing intensity of sound as it approached the school during random searching. This is a matter distinctly different from following up a sound gradient, the phenomenon whose existence has been questioned by van Bergeijk.

In order to present some idea of the areas and limits of the near-field and far-field effects and their somewhat complicated relationships, the following comments and calculations are given.

How far near-field directional cues extend from a sound producing source will, to a considerable extent, determine their utility to the listener. This distance varies with the frequency, being greatest at low frequencies and least at high, and with the amount of the energy output of the source. For instance, holding the energy output constant, through the temperature range at which *Galeichthys* emits its characteristic "percolator"⁴ sound, approximately between 20 and 30°C, a frequency of 1000 Hz has the calculated limit of its near field between 9½ and 9¾ inches from the origin, respectively. Other values in feet follow:

Temp.	Frequencies in Hz				
°C	25	100	200	300	800
20	31'+	7'+	3'+	3'-	1'+
30	32'+	8'+	3'+	3'-	1'+

These relationships were calculated from the given temperatures and frequency by means of the empirical equation of Albers (1960).

$c = 141,000 + 421t - 3.7t^2 + 110s + 0.018d$, where c = velocity in cm/sec, t = temp. in °C, s = salinity in ppt and d = depth below surface in cm. Using $s = 34.8$ ppt and $d = 150$ cm, values of c were calculated for various values of t . Changes in s and d were negligible for present purposes and were held at the values given, reducing the equation to

$$c = 145,829.7 + 421t - 3.7t^2.$$

The values of the wavelengths were obtained from the relationship

$$\lambda = c/f$$

where λ = wavelength and f = frequency in Hz. From van Bergeijk (1964) the point of equal

⁴So designated by Kellogg (1953).

amplitude of the pressure waves and the displacement waves, from a pulsating bubble, which he indicates as a convenient measure of the range of the usefulness of near-field effects, were calculated from the expression

$$n = \lambda/2$$

where n = the distance of the point of equal amplitude from the point of origin.⁵ The values obtained are, of course, rather rough approximations, but are fully adequate for the present discussion. The data on the temperature range at which *Galeichthys* is sonic are original, having been established for a certain locality in connection with another project, only vaguely related to studies on schooling. Differences in the attenuation of the various wavelengths concerned are not significant within the spread of frequencies here discussed (Albers, 1960). At much higher frequencies, that is, within the k Hz. range, there is some differential absorption, but this is far removed from the sounds fish usually produce. It should be emphasized, however, that these calculations do not include the influence of the absolute energy of the original signal which, of course, can be of great importance.

Since the range of hearing in fishes has been calculated in general terms to run from about 100 to 3,000 Hz and the range important to the lateral-line organs from about 20 to 500 Hz (Harris, 1964), it follows that the statements made here all fall within the accepted range of fish auditory powers. Also, that when the producer is separated from the receiver, "... both near-field and far-field effects must be considered for the organs of hearing as well as the organs of the lateral line." At a frequency of 25 Hz, the wavelength is about 200 feet and at 1000 Hz it is about five feet.

From the preceding it should be possible to estimate at about what distance a fish would lose the directionality of, say, the percolator sound by knowing the frequencies and temperatures involved. Tavalga (1960) stated that there was a predominance of frequencies around 300 Hz in these sounds, and his sonogram indicated that they ranged to below 100 and above 800 Hz. If a fish loses its sense of directionality at about the distance calculated, then if a fish was receiving cues from a *Galeichthys* producing the "percolator" sound at a frequency of 300 Hz or higher, it would not be useful beyond something less than three feet. However, in the spectrum of this sound there are abundant frequencies of 200 and some of less than 100 Hz. Presumably

these would be considerably more attenuated at their respective ranges which are about three and one-half and eight feet. At a frequency as low as 25 Hz the range reaches some 30 feet, and one may assume that there are some effective frequencies between these two extremes, at perhaps ten to 20 feet from the sound source. At this distance the ability to receive directional cues, especially at night, could be of great value, as will be developed, especially since there is some observed behavior of fishes that may be accounted for by a range similar to the one given above. In a personal communication, Dr. Tavalga indicated that he has also observed differences in the behavior of both "lost" schooling fishes and predators that could perhaps represent a passing out of or into the limits of the near-field.

Other influences

Other sensory modalities, such as olfaction or taste, would not seem to be importantly involved in the interactions of schooling fishes and their predators, if at all, or at least there is no clear evidence or theory which would indicate such involvement. Brock and Riffenburgh (1960) considered olfaction a possibility, writing, "... predators may attempt to remain with a school of prey even though satiated, and it is not unlikely that a large school of prey may leave an easily detectable trail of odor for a predator to follow," but present no data to support this opinion. Skinner, Mathews and Parkhurst (1962) concluded that the *Schreckstoff* effect served to warn other members of a school, because "... alarmed fish communicate fright by releasing a chemical substance into the water." This statement was questioned by Williams (1964) as follows, "Why then for communicating a message for which speed of reaction would be especially important, would fishes rely on the slow process of chemical diffusion?" With apparently a single exception, the *Schreckstoff* reaction is confined to the Cypriniformes, an almost entirely freshwater order. This group does exhibit some schooling, usually in a facultative form. Fishes of this group are not to be considered as obligate schoolers. Strangely, in this connection, Thines and Vandenbussche (1966) indicate that in *Rasbora* the alarm substance is more effective in the daytime, even in a dark room. Pfeiffer (1962) has reviewed the entire subject of the "fright reaction" and his analysis indicates it to be rather remote from the present problem.

Breaks in ontogeny, or more properly, points at which step functions occur, such as in the case of certain fishes, pelagic from hatching,

⁵ n is expressed in the same units used to measure wavelength.

when they reach a sufficiently advanced but still transparent post-larval stage, and encounter shallow water, will permanently change their attitudes, develop pigment and settle close to the bottom. These, at this time, usually break up their schools into single individuals or small parties, as the life history unfolds. This type of ontogenetic change seems to be present in a life history where one stage is required to vanish abruptly, so that the species concerned either becomes a permanent schooler or abandons the habit entirely.

THE STRUCTURE AND SIZE OF SCHOOLS

Brief reference has already been made to the range of visibility under water and the relation of the conspicuousness of fishes to its degree of transparency. Here a return is made to that subject and its more immediate implications. Because of the considerable mathematical difficulty of dealing with three-dimensional structures of complex outline, see Cullen, Shaw and Baldwin (1965), the case of a simple surface type school, which is often not more than one or two fish deep, will be discussed for illustrative purposes.

It is not merely accidental that most fusiform fishes, not in a school, usually face toward any disturbance less than one that instigates immediate flight. Aside from visual demands in an animal that cannot turn its head alone, there is an immediate reduction of conspicuousness, as the frontal view is much less conspicuous than the corresponding lateral aspect. Anyone who has operated under water is well aware of the phenomenon of having a fish effectively disappear before one's eyes merely because it had turned so as to point at the observer. Such turning to face a disturbance is much less likely in the case of a chunky fish such as an ostracid or diodontid in which such a maneuver would do little to alter its aspect. These, moreover, are distinctly non-schooling types.⁶

The shape of schools

Since circles and spheres enclose the maximum amount of area or volume respectively for a given perimeter or surface, it follows that these or other shapes have a distinct bearing on the conspicuousness of fish schools and aggregations. For these reasons it could be argued that the commonness of such approximations as are found in real schools is a result of selection. As has, however, been indicated in other connections, it happens that many non-living

systems show the same kind of behavior which depends only on their innate cohesiveness. That is, a drop of suitable oil in water of the same specific gravity will be found to be spherical or a drop of mercury on a flat surface will be found to be a badly deformed sphere, flattened on one side and of other curvature on the top side. In other words, departures from the form showing minimum surface may be considered as a measure of some special influence. In this sense the spherical schools discussed by Breder (1959) and the flowing schools of Breder (1951) all could be following simple physical influences, with the first presenting the least conspicuous form possible and the second exposing a much greater area. The latter are usually seen in very shallow water, commonly shallow enough to eliminate the species' predators. Also with the bottom and water surface so close together only globular groups of small size could occur, as for instance the globular pods of *Plotosus* reported by Knipper (1953 and 1955) and observed and discussed by Clark, in a personal communication. However, large sheet-like schools can naturally "fit" most easily into such vertically limited environments. Where this dimension is greater, schools tend to deepen, culminating in approximate spheres of some bulk. Here also larger predators may swim and view such gatherings from greater distances, up to the point where visibility ceases and the schools have protection not so much based on their own geometry as on the peculiarities of underwater vision. Springer (1957) considered huge schools of small fishes, whose bulk at a little distance could resemble some single large creature, to have a discouraging influence on possible predators. This would represent a case where visibility instead of invisibility became of positive advantage to the schoolers.

The problem of enormous schools

Data on details relevant to the present studies are not yet available on the truly huge schools, often involving many thousands of fishes, as exemplified by the great assemblages which are frequently formed by *Clupea* and *Scomber*. Suggestive information, however, would seem to indicate that they are not as uniform in their size composition as smaller schools are usually seen to be. It is conceivable that such lack of uniformity may be based on the manner in which they develop. If so, it may be that they represent an agglomeration of all the smaller schools in a given area. If, say, several hundred schools, each normally uniform in size range within itself, merged with others acceptably similar, it could cause the assembled mass to show a larger variation, from place to place

⁶ All these comments are related to the less specifically expressed view of Allee *et al.* (1949) and Allee (1951) on the reduction of total area exposed by fishes in a school.

within the whole group. If the combined schools mixed sufficiently, large fish encountering much smaller ones, a disruptive influence could develop, or at least induce an internal realignment so that the large fish were somewhat restricted to one part of the group and the small to another part, with intermediate fishes bridging between them. Then more or less temporary gradients in respect to size, or other characteristics, could develop and stream about within the group, establishing a continual movement driven by the realignment activities of all individuals. This sort of continual adjustment, with respect to locomotor facility is actually to be seen, on a much smaller scale, in smaller schools, and Breder (1965) thought that it formed the basis of the continual small adjustments found in most ordinary schools. This could easily lead to a shearing action breaking up the different size-groups into smaller, but still large schools. Such effects may in fact be responsible for the eventual disintegration of gigantic schools.⁷ Also, it has been shown by Hunter (1966) that angular divergencies between school members are greater between individuals of greater variation in size.

Milanovskii and Rekubratskii (1960) performed some experiments with *Phoxinus* that have an indirect bearing on the preceding comments and on the amalgamation and disruption of groups composed of merely facultative schoolers, as follows.

"We noted that under natural conditions, several schools of minnows which fed in the same place, and which appeared from the outside to be one unit, reacted differently to changes of the surrounding environment. In the beginning of our observations, a school of small minnows was feeding; then a school of larger minnows approached cautiously, followed by the school of largest minnows, even more cautious and rapid than the fish of the first two schools. All the fishes, small, medium and large, mingled together and had we not seen them approaching gradually we might have considered them to be a single school. However, after some time, the large minnows hid behind the nearest stone, which they found somewhat downstream. From their hiding place, they swam to the food, grabbed it, and swam back. Such a phenomenon of utmost cautiousness in the search for food we designated by the term "withdrawal." At the slightest movement of the observer, the large

minnows swam away, while the small and medium-sized ones continued to feed undisturbed. When the experimenter stretched his hand over the feeding spot, the school of medium-sized minnows fled while the smallest remained, fleeing only after the hand was immersed in the water. Thus, fishes of three different schools reacted in different ways to changes in the environment, while fishes belonging to each of the three schools reacted as one whole. The natural movements of fishes, obtaining food, fleeing in the face of danger, etc., have definite signal values (of different orders of importance) for the remaining fishes of the school. Among these movements one can distinguish between searching movements, alimentary movements and movements of fear." Also they wrote, again of fishes in a stream, "The strongest biological signal is the natural movement of fear. If, being frightened by something, one or several fishes move aside, the whole school follows them. We tried to give the fishes food in such small quantities that only one or two fishes could obtain it. Once satiated, these specimens became more fearful and went to shelter; they were followed by all the other, still hungry, fishes."⁸

The bearing that the various preceding notes have on ideas concerning the survival value of schooling is, among others, as before intimated, that such massive groups may have a deterrent influence over approaching predators.⁹ However, it is also reasonable that such an influence would wane in a short time, to be replaced by an opposite one based primarily on habituation of nearby predators to such tremendous schools. The slow drawing in of predators from perhaps a considerable distance would be expected to follow, because individuals of the prey species concentrated in one place in an enormous mass would proportionally restrict their numbers elsewhere. Thus, a situation of positive survival value could transform to a negative one, and possibly also could become a force for the disintegration of the huge group.¹⁰

⁸ These observations are also related to those of Breder (1965) on the feeding of schools of very small *Mugil*. The avoidance reactions these workers described is, no doubt, caused at least partly by the general refusal of fishes of slightly different sizes to mix.

⁹ Such a situation is probably related to or identical with the "confusion effects" of Allee *et al.* (1949) and Allee (1951). Also related to this is evidence that fishes eat more when in groups than when alone (Allee, 1938).

⁷ The finding of Allee and Dickinson (1954) that when a *Mustelus* was as little as 6.7 per cent smaller than another, the lesser dogfish would avoid the greater. This does not imply aggression on the part of the large fishes. This kind of avoidance is basic to the matters discussed above.

¹⁰ According to the English translation of Nikolsky (1963), the Russian usage is to apply "shoal" to such large groups as those here under discussion and to limit "school" to groups so small that presumably all members could have visual or other contact with every other member. In English and American usage "shoal" has apparently always been used as a synonym of "school."

The maximum advantage, then, is enjoyed by relatively small groups; that is, with additions of a few fish to a small group, the conspicuousness of the assemblage increases at a much smaller rate than does the number of its members. This advantage is lost, however, when the number becomes so vast that the volume occupied by the group, although remaining proportional to the number of individuals, becomes a conspicuous mass in terms of absolute size.

These various factors are necessarily influential in limiting the sizes of fish schools. Field observation demonstrates that in a wide variety of species this vague but very real "limit" is not very large, at least under normal circumstances. Although Breder (1965) could find no theoretical upper limit to the size that a fish school might attain on a hydrodynamic basis, such limitation may well be rooted in the aspect here under consideration.

Williams suggests that the tendency for schools to increase in size without limit until "... the advantages of increased gregariousness would be balanced by some disadvantage, such as depletion of food in the center of a school." This is something that under ordinary conditions would call for an extremely large school because of the internal churning of schools, exposing first one and then another of its members to the periphery as well as the general conditions of having the school move about or holding a position in a flow of water through it.

MacFarland and Moss (1967) were able to measure dissolved oxygen within and outside of large schools of *Mugil cephalus* Linnaeus. They report that there was a reduction of the oxygen concentration within the schools. Also that there were areas of disruptive activity in the locations showing the lowest oxygen readings. These areas sometimes broke up into several smaller schools. They refer such intra-school activity to oxygen depletion, carbon dioxide increase and pH reduction. As they indicate, this could account, at least in part, for such behavior and may be a factor in limiting school size on a basis of respiratory need.

Here the problem of mill formation originally analyzed by Parr (1927) and extended by Breder (1965) is pertinent. Does mill formation actually have deleterious¹¹ effects on the fish in a school or is an occasional occurrence of it without significant effect on them, making an interest in mills merely a matter of the mechanics of its origin and eventual destruction? This

¹¹ These could be extrinsic, possibly leading to greater predation for instance, or intrinsic, holding the fish uselessly or dangerously in a place of poor feeding or other disadvantage.

will have to remain an unanswered question, as so far there appear to be no facts or ideas that could begin a structure of theory building.

THE RELATIVE SIZE OF PREY AND PREDATOR

The manner of feeding of predators on schools would seem to have a distinct bearing on the success of the school as a survival device. Commonly predator fishes may be seen to dash into a school and pick off an individual member and immediately retreat, usually swallowing the fish whole. The predator seldom takes more than one fish at a time, but returns again and again, apparently until satiated. Typical examples of this type of predator are *Caranx*, *Tylosurus* and *Sphyræna*. This type of feeding is probably the least disruptive and the most conservative of the predators' food supply.

Other manners of feeding on schools, as that shown by *Pomatomus*, is destructive of much more of the food supply than that described above. Commonly an individual *Pomatomus* or small group of them will race through a school of smaller fishes, snapping right and left while they go, leaving a trail of half-fish behind. Usually it is the anterior end that is left, and this probably means that less than half of each fish destroyed becomes food for the predator.¹² Similar modes of "wasteful" feeding on schooling fishes have been described by Rich (1947) for *Xiphias*, and Breder (1952) for *Pristis*. Wisner (1958), however, exonerates *Makaira* from such destructive activity, as flailing about with its elongated rostral process in a school of much smaller fishes.

In fishes the ratio of the size of prey to predator may vary widely, ranging from extreme cases where the predator may be more than 20 million times the weight of its normal prey's weight, as for instance *Manta* preying on near microscopic plankton.¹³ From this extreme the ratio ranges to unity or even to cases in which the prey may be larger than the predator, as in *Histrio* and the extreme example of *Chiasmodon*. This range of differences in size has a bearing on the nature of the utility of schooling.

The phenomenon of herding, for instance,

¹² These mutilated fish-remains usually become food of other types of fishes or invertebrates which otherwise would be scavenging for other organic matter. Occasionally some of them survive but are no longer members of the schooling population. See Breder (1934) and Gunter and Ward (1961) for records of this sort.

¹³ Based on a *Manta* of 3,000 lbs. compared to a plankter of 0.1 oz., which is probably much too heavy for the average plankton organism. The value given for the difference in size is certainly minimal, possibly even 3 to 5 times too small.

can only take place within certain relative size ranges between prey and predator, for if the two be of approximately the same size, the predator's approach becomes one of stalking, and if the prey is vastly smaller, as above noted for *Manta*, it becomes a matter of ranging about in search of streaks of plankton where neither stealth nor herding is involved.¹⁴

SCHOOLS, THEIR MODELS AND DISCUSSION

The only serious mathematical treatment of the possible protective value of schooling has been presented by Brock and Riffenburgh (1960). See also Brock (1962) for supplementary data. This was followed by a note from Olson (1964) who called attention to the work of Koopman (1956a and b and 1957). The latter, which is concerned with the development of "the theory of search" from the mathematical approach, discusses cases involving situations where both target and searcher are moving, as in naval battles. Olson recognized the identity of this with the situation of prey and predator, especially among oceanic fishes. The contributions of both Brock and Riffenburgh, and Koopman are given in convincing mathematical terms.

The usage of the word "school" by Brock and Riffenburgh and by Olson is different from the usage here employed, both in implication and in context. In their usage, a school of fish covers both schools and aggregations as here used, irrespective of the individual orientations or the distances between individuals, up to the limit of the range of visibility and without reference to the drives and circumstances that created the group.

As the equations of Brock and Riffenburgh do not take the orientation of individuals into account, they apply equally well to either polarized or non-polarized assemblages. One of the marked characteristics of schools, in the present sense, is that they consist of individuals spaced a "standard" distance apart. Thus equation (28) of Brock and Riffenburgh is applicable to schools only when c , the distance between individuals in the group, is very small, for if it becomes large, the polarization loosens and the group can no longer be recognized as a closely ordered array of fishes, all swimming side by side in a common direction. This distance, (axis to axis between adjacent fishes) is usually from

one-half to three-quarters the length of the individuals (Breder, 1954, 1965).

The whole possible confusion is further complicated by the fact that Brock and Riffenburgh, although dealing with "... assumptions ... and conclusions ... not related to the observed behavior pattern of any particular species of fish ...," obviously are concerned primarily with scombriform fishes, a group with which the senior author of that paper has had wide experience. These fishes form excellent material for such studies, being one of the notable schooling groups. It so happens, however, that as many of these species age they tend to lose their strong propensity to school. Consequently, at least in the larger species such as *Thunnus*, the giant-sized individuals occur as solitary fishes or at least do not form the tightly organized schools of their youth. Large fishes in general tend less toward schooling than do small ones. This may be associated with the fact that the larger the fish, the less likely it is to fall prey to some predator of still larger size. Certainly if schooling serves a protective function, the above should naturally follow.

Lest any of the above comments be thought a criticism of a very thoughtful piece of work, this is to emphasize that these remarks are given here only as a warning to the reader to beware of possible misunderstanding because of differences in the usage of terms.

Koopman (1956a and b, 1957) divides his work into three parts, which he describes as follows. "I. The kinematic bases, involving the positions, geometrical configurations, and motions in the searchers and targets, with particular reference to the statistics of their contacts and the probabilities of their reaching various specified positions. II. The probabilistic behavior of the instrument (eye, radar, sonar, etc.) when making a given passage relative to the target. III. The over-all result—the probability of contact under general stated conditions, along with the possibility of optimizing the results by improving the methods of directing the search." Koopman considers much of his theory concerned with the probability of situation to be a special case of the theory of stochastic processes. Obviously much of this has direct bearing on predator and prey relationships, especially as displayed by open water fishes.

Both Brock and Riffenburgh, and Olson express regret for the small amount of field data available to compare with mathematical models. The former wrote, "The general lack of field data concerning the behavior pattern for a prey species and its predator renders either the confirmation or refutation of conclusions reached

¹⁴ See Bigelow and Schroeder (1948) for a discussion of herding in *Alopias* and Hiatt and Brock (1948) for a discussion of it in *Euthynnus*. More complex prey-predator relationships are described by Springer (1957) for *Rhincodon* and others, by Fink (1959) for Porpoises and *Sardinops* and by Bullis (1961) for *Carcharinus longimanus*.

in this paper by the elaboration of some scheme of predator strategy rather futile." The latter wrote, referring to the Koopman equations, "These are two basic equations, but to put reasonable numbers in them is another matter." For similar reasons, no attempt will be made here to apply any of these equations. Our intent is to bring together the mathematical and observational aspects of work on fish schools, to present some field observations hitherto unpublished, and to give some general considerations on the whole matter.

Although there is a large literature on prey and predator relationships, almost none of it is concerned with features that would seem to have bearing on the problems of fish schools. The work on bird flocks, such as those formed by starlings, indicates that these are evidently operating in a similar manner about as closely as could be expected, considering the large basic differences between birds and fishes, see for instance Horstmann (1950).

In discussing the possible evolutionary course of the schooling habit Williams wrote that "... the lack of any apparent functional organization is an eloquent argument for the conclusion that the properties of schools have not been established by natural selection on a basis of survival values." By "functional organization" Williams means any or all specializations such as "alarm notes," markings displayed in flight, *et cetera*. His detailed comments on the above are followed by, "Evidence for such mechanisms in fish schools would invalidate my position on their lack of functional organization." This extreme position is here considered, at least, premature, as there are a number of valid instances when just such mechanisms seem to be indicated. Considering the difficulties in obtaining adequate data and in interpreting their significance, the slow progress in this direction is not surprising. Relevant evidence suggestive of just such "functional organization" is to be found in practically all the current work on sound production among aggregating and schooling fishes, such as seen in Fish (1954), Kellogg (1953), Moulton (1956, 1958, and 1960), Tavalga (1958a, b, c and 1960), Marshall (1962), Stout (1963a and b), and Winn (1964). The consensus of these workers is in general that there are two primary functions provided by the sounds produced by fishes, evidently being either of sexual or social significance. The evidence that sound production is relevant to organization is indicated by various schooling fish that become sonic only at night, when the visual system is inoperable or only feebly so (Takarev, 1958; Shishkova, 1958; Moulton, 1960; and Marshall, 1962).

Bearing on the question of functional organization of fish schools are recent, more refined measurements of the spacing of individuals in a school that have shown that both extrinsic and intrinsic influences can vary these distances. John (1966), working on *Tilapia nilotica* (Linnaeus) and *Notemigonus crysoleucas* (Mitchill), for instance, showed that at very low light levels, below 10^{-3} f. c., schools tended to break up and that individuals served as, "... mutual distractions for one another and also as sources of fright." Previously, it had been thought that schools in little light broke up merely because of visual difficulties. This indicates that there is a positive repelling factor involved, that appears as light fades.

Hunter (1966), by means of computer techniques, showed that schools of *Trachurus symmetricus* (Ayres) deprived of food swam at greater distances from each other than did the same fishes after feeding. Although schools and aggregations appear to be leaderless, there are some special cases, such as a white *Carassius* being the focal point for aggregating by yellow companions (Breder, 1959).

There is no disagreement with the Williams' view of how schools may have arisen, namely "... that schooling could be expected to arise in any species subject to aggregation." In accordance with Williams' definition of schooling, this means, in effect, that fishes drawn to a given area by some non-social influence may then in some cases become social. He also wrote, "... that a school is not an adaptive mechanism itself, but rather an incidental consequence of adaptive individual behavior. The adaptation is the reaction of each individual to the school."

It seems most likely that schooling in fishes arose from a wide variety of causes, including some that are purely mechanical (Breder, 1965). Further speculations on this matter would seem hardly to be worthwhile, until some time when data and theory have reached a higher level of development.

Evidently the schooling habit becomes established because of purely mechanical or biological reasons, but it would certainly be expected that gene flow could re-enforce the habit, if it proved to be advantageous to the group.

Levins (1962, 1963, 1964) expresses the idea that the adaptive significance of gene flow is that it permits appropriate response to long-term general fluctuations of environment, while "... damping the responses to local ephemeral oscillations." This undoubtedly has bearing on the distribution of fish assemblages of all kinds. Levins indicates that migration tends to increase the above condition. It is noteworthy in this connec-

tion that obligate schooling forms generally have a large geographic range, produce large numbers of young and commonly show migratory movements. The population density is, of course, extremely high within the limits of the close confines their schools delimit. It is, however, extremely thin if their numbers are considered in reference to the huge areas the schools pass over, even more so if extensive migrations are involved. The fact of schooling precludes nest building or other protective reproductive modes that presumably permit the production of fewer young. The formation of great schools, and their subsequent dissolution, as discussed herein, may well exercise a regulatory role in the gene flow of the species involved.

All that precedes in this paper could be used to support the view that the functioning of prey-fish schools, as well as of unpolarized aggregations, represents just another method of attaining a manner of behavioral homeostasis. This implies that schooling is effective against excessive predation through a wide range of activities, but fails when various limits are exceeded. Backed up by adjustment of reproductive potential, all under the control of selective processes, including those of both predator and prey, as parts of a dynamic system, it is evidently sufficient to produce a situation of considerable stability in the observed populations. While these systems are probably not as closely controlled as, for instance, the hydra populations of Slobodkin (1964), it would be extremely difficult to attempt such analysis and experimental procedures on schooling fishes as he gives his material. Nevertheless, it would seem that the basic activity is similar. This view accepts schooling as a biologically useful activity seen against the appropriate ecological background.

SUMMARY

1. The range of sight, limited as it is by transparency of the water and the amount of light present, governs the effectiveness of schooling as a form of predation control, which varies widely with environmental features.

2. The geometry of the school shape and its motion affects the conspicuousness of schools where water transparency permits good visibility.

3. In situations where visibility is not a limiting factor, the system presents the degenerate limit where schooling fails to protect effectively.

4. The general quietness of fish schools, except under special conditions where some sound may be inevitable or others in which it may be desirable, suggests that there may have been suppression of sound in schooling fishes, probably by way of selection.

5. The physical form and attitudes of the constituent fishes bear on the effectiveness of schools as a protective device, as do the shape and motion of them, schooling being associated chiefly with streamlined fishes, less often with chunky or odd-shaped fishes.

6. Sufficiently large schools may act as a repellent to predators because of their size and shape.

7. School size is related to the availability of fishes of sufficient similarity of size to compose a coherent group, as well as the mechanics of flow within the group, and to this extent becomes amenable to treatment by hydrodynamic means.

8. The size of the predators relative to the size of the prey leads to "stalking" if the sizes are about equal and to planktonic sifting if the prey is extremely small compared with the predator.

9. The whole matter of schooling and aggregating is looked upon as a mechanism of behavioral homeostasis and as such is subject to the influences of selective processes.

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5

Longevity of the *Naja naja philippinensis* Under Stress of Venom Extraction

ENRIQUE S. SALAFRANCA

*Serum and Vaccine Laboratories, Bureau of Research and Laboratories, Department of Health,
Alabang, Muntinlupa, Rizal, Republic of the Philippines*

(TEXT-FIGURES 1-3)

I. INTRODUCTION

IN order to ensure an adequate and uninterrupted supply of good quality venom of the Philippine cobra, *Naja naja philippinensis*, for antivenin production, the Serum and Vaccine Laboratories (SVL) in Alabang, Muntinlupa, Rizal, under the Bureau of Research and Laboratories, Republic of the Philippines, maintains a serpentarium. On a few occasions, requests for venom for medical and research purposes have been received and have been accordingly filled. The presence of cobras in the laboratory has every now and then attracted visitors. They include foreigners and Filipinos, mostly students, laboratory workers, and laymen. Some of them seek information regarding cobra venom and cobra antivenin production while others merely wish to see the cobras out of curiosity.

The principal interest of the laboratory, besides maintaining an adequate supply of the venom, is to find out how long the cobras usually live in captivity and how the stress of venom extraction affects their longevity. It is expected that the information gained in our serpentarium will make it possible to prolong the life expectancy of these animals and increase their lifetime venom yields under the conditions at the SVL serpentarium. This study was conceived and carried out for that purpose.

A review of the literature for the longevity of cobras under the specific conditions to which cobras kept in serpentaria for their venom are subjected has yielded negative results. References encountered so far regarding longevity of

snakes are those of Baker (1951), Loveridge (1946), and Schmidt & Inger (1957).

Baker recorded a captive Pacific rattlesnake (family *Crotalidae*) that lived for 20 years, but doubted that wild ones could reach such age. He further stated that few diamondbacks (genus *Crotalus*) live past the first winter. Loveridge states that apparently the record of longevity for cobras kept in captivity is held by the two specimens which lived for 13 years at the New York Zoological Park. Schmidt and Inger state that the greatest age on record for the reticulated python (*Python reticulatus*) is 21 years; for the Indian python (*Python molurus*), 17 years; for the African python (*Python sabae*), about 15 years. In captivity, the diamond python (*Morelia argus*) is known to live a little more than 4 years.

J. H. Mason,¹ superintendent of the serum department, South African Institute for Medical Research, speaking about their serpentarium, states that they milk their snakes once every fortnight and that "the death rate is rather high as is usual when snakes are crowded together and milked frequently."

Cobras, like most wild animals, are very nervous especially when confined in limited enclosures in relatively great numbers. As in the case with our serpentarium, where they have to be maintained to ensure a continuous supply of venom for immunization, many have even refused to eat and literally starved themselves to

¹Personal communication, 1957.

death. The presence of men, cobra tenders and visitors, and frequent handling for venom extraction all contribute to increased irritation. All these factors, especially the latter, seem to exhaust them and shorten their lives.

II. MATERIALS AND METHODS

A total of 2,075 cobras, *Naja naja philippinensis*, were observed to supply the data for this paper. These were collected during the period December 3, 1959, through April 16, 1963. Except for occasional specimens caught within and around the laboratory premises, all were from the province of Camarines Sur, Island of Luzon.

No attempt was made to determine the ages of the specimens used inasmuch as no information which may be used as a practical age indicator was available to the author. Only specimens 36 inches or more in apparent good health and with intact fangs were used in this study. These were caught in a manner to avoid any injury to them. The maximum size noted was 59 inches with an average length of 42.73 inches among 393 specimens measured at random.

A. Care and Management

The care and management of the cobras at the SVL serpentarium conform with the facilities available and the specific purpose for which they are maintained.

1. *Housing*.—The laboratory maintains two roofless enclosures for housing these snakes. The larger one measures 44.3 feet by 27.3 feet, surrounded by a four-foot-high concrete wall and five-foot-high reinforced half-inch mesh wire screen atop the concrete wall. The inner surface of the wall inclines inward so that a plumb line dropped from the inner surface of the upper end of the wall falls about four inches from the inner surface of the bottom of the wall. The walls have a two-and-a-half-inch overhang all around the inside.

In the center is a rectangular tiled trough, 77 inches by 58 inches and 5 inches deep, which is filled with water from a fountain. Here the snakes usually water themselves after venom extraction and at other times. Along the base of the walls inside the enclosure is a concrete strip 15½ inches wide. On this are distributed blocks 16 inches by 8 inches by 4 inches in dimension. Each block has twin hollows, 2 inches by 5½ inches by 8 inches. In these hollows, where it is generally cool and dark, the snakes remain most of the time. The rough surface and corners of the blocks provide convenient anchors for their skin when they start to molt.

The smaller enclosure measures 22.6 by 25.3 feet. The surrounding wall is 3.7 feet high with a 9-inch overhang on the inside. The reinforced wire screen atop the wall is 3.8 feet high.

The tiled trough in the center is 35 inches square and 3.6 inches deep. It is filled with water from a fountain in its center. Hollow blocks are also provided as in the larger enclosure.

2. *Feeding*.—White mice are made available on the days following venom extraction for the snakes to feed as they please.

3. *Collection of the venom*.—The preparatory steps employed for controlling the snake have been described elsewhere (De Leon & Salafranca, 1956).

The cobra is grasped gently but firmly by the neck behind the angles of the jaw, with the thumb and index finger assisted by the remaining fingers of the left hand. The tail end is controlled by the third and small fingers of the right hand, with the thumb, index, and first fingers holding the beaker for venom collection. The latter is a "Pyrex" 100 ml. (50 × 65 mm.) beaker. A rubber diaphragm, a circular piece of all-rubber surgical sheeting or the intact portions of discarded inner tube (26" × 2.125") of a bicycle tire of appropriate diameter, is tautly secured across the opening of the beaker with a piece of strong cotton twine. The diaphragm prevents the fangs from jamming against the wall of the beaker during the bite and thus prevents them from breaking off, and because the snake is not hurt in the process it bites more fully and holds the bite longer than with the method and collection apparatus previously employed (De Leon & Salafranca, *ibid.*). The diaphragm also prevents contamination of the venom with saliva, soil, and other debris present in the mouth of the snake.

As the beaker is brought opposite the snake's head, the cobra generally opens its mouth and voluntarily bites. At times it appears to be so eager to do so that venom spurts before it actually bites (the *Naja naja philippinensis* is a "spitting" cobra). The fangs pierce the rubber diaphragm and the venom may spurt out in a fine stream with enough force to cause previously collected venom in the beaker to froth, followed by a few drops, or a trickle may be noted along the wall of the beaker, or it may come out in isolated drops.

Venom was collected once fortnightly, except as indicated in the following controlled experiments:

1. *Effect of different schedules of venom extraction on longevity*.—In order to determine the effect, if any, of the frequency of venom extraction on longevity, replicate experiments were

conducted on comparable groups of cobras, which were subjected to different schedules of venom extraction.

In the first experiment a batch of 114 cobras was divided at random into three groups of 38 each. Venom was extracted once a week from the first group, once in two weeks from the second group, and once in three weeks from the third group. All the snakes were allowed to move freely in the larger enclosure and venom col-

lected according to the schedule indicated until all of the specimens died. Color bands were painted on the snakes to identify the different groups.

A second experiment and a third, following exactly the same plan, were conducted with a batch of 192 cobras divided at random into three groups of 64 snakes, and another batch of 90 divided into three groups of 30 (Table I, Fig. 1).

TABLE I.
RELATION BETWEEN LONGEVITY AND THREE SCHEDULES OF VENOM EXTRACTION

Experiment Number	Schedule of Venom Extraction		
	A Once a week	B Once in 2 weeks	C Once in 3 weeks
Experiment I 38 cobras per schedule	39.79*	51.53	59.03
Experiment II 64 cobras per schedule	56.06	94.35	123.81
Experiment III 30 cobras per schedule	48.70	63.63	84.40
Over-all averages	48.18	69.84	89.08

*The figures under each schedule in each experiment are expressed in number of days and represent the arithmetic average of all the respective data collected.

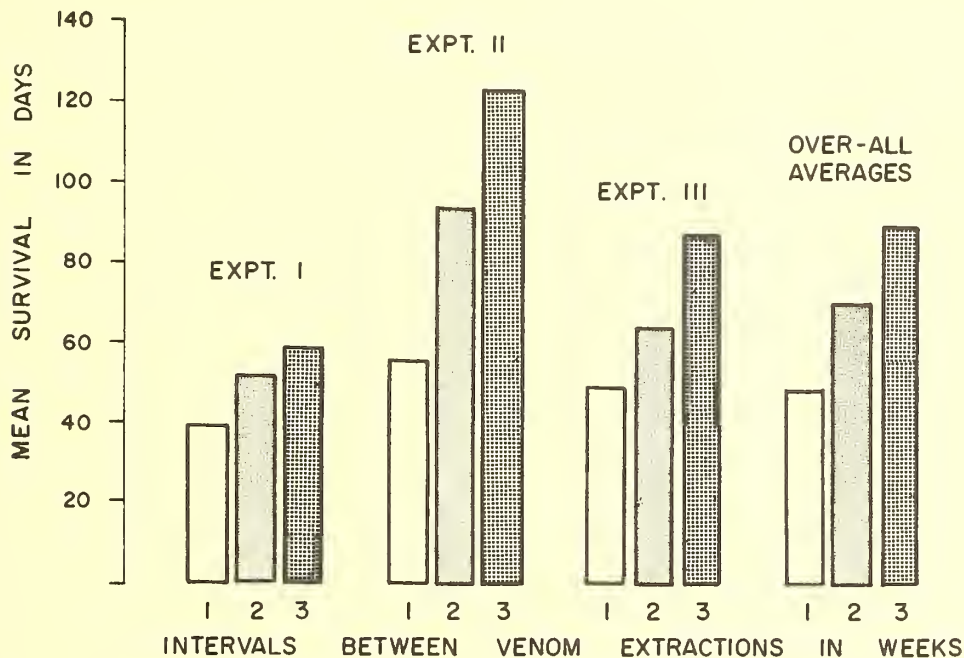


FIGURE 1 COMPARATIVE MEAN LONGEVITY OF COMPARABLE GROUPS OF COBRAS UNDER THREE SCHEDULES OF VENOM EXTRACTION IN THREE EXPERIMENTS

II. *Comparative longevity of cobra under stress of venom extraction and of those from which no venom was extracted.*—A batch of 40 cobras was divided at random into groups of 33 and 7, respectively. From the first group, venom was extracted fortnightly; from the second no venom was extracted. The number of cobras in the second group was kept as small as possible mainly for economy reasons. All were kept in the same enclosure under the same conditions until all had died. The comparative data are presented in Table II.

III. *Death rate and time (month) of the year.*—To determine any possible relation between the time of the year and the death rate, beginning-of-the-month inventories were determined starting with December, 1959, through July, 1963. Any acquisition during the month was added to the corresponding inventory to arrive at the monthly population figure. The total number of

deaths during the month was determined and the monthly mortality rates were computed over a period of 43 months, January, 1960, through July, 1963 (Fig. 3).

In going over these observations and evaluating the data collected, one must be reminded of the possible error which a greater or lesser percentage of carry-over of the specimens from one month to the other, and consequently the relative ages of the specimens carried over from month to month, may have on the resulting percentages.

IV. *Longevity and time of collection.*—In an attempt to determine whether the time of the year the snakes were collected had any influence on their subsequent longevity, the data on all the batches included in this study and which were subjected to a uniform, fortnightly schedule of venom extraction were compiled and are presented in Table III for this purpose.

TABLE II.
LONGEVITY OF COBRAS UNDER STRESS OF EXTRACTION COMPARED WITH THOSE FROM WHICH NO VENOM WAS EXTRACTED

Group	Number of Cobras	Schedule of Venom Extraction	Longevity in Days		
			Minimum	Maximum	Mean
I	33	Once in 2 weeks	39	118	74.90
II	7	No venom extraction	31	226	149.14

TABLE III.
LONGEVITY IN BATCHES OF *Naja naja philippinensis*, ALL SUBJECTED TO FORTNIGHTLY VENOM EXTRACTION

Number	Date of Arrival	Total No. Specimens	Minimum	Maximum	Mean
I	December 3, 1959	229	5	147	94.67
II	March 8, 1960	491	2	202	87.86
III	June 7, 1960	555	2	175	84.31
IV	October 17, 1960	38	13	94	51.56
V	December 22, 1960	65	41	131	91.58
VI	February 9, 1961	30	7	90	50.70
VII	June 21, 1961	55	7	91	50.70
VIII	September 6, 1961	109	12	120	64.04
IX	December 22, 1961	24	31	105	82.79
X	January 29, 1962	29	74	142	102.31
XI	April 23, 1962	32	63	114	86.96
XII	June 25, 1962	32	57	131	83.78
XIII	September 4, 1962	29	23	118	54.28
XIV	November 4, 1962	15	63	97	73.33
XV	January 14, 1963	33	39	118	74.90
XVI	April 16, 1963	38	27	146	79.34
Total		1,804			
Over-all averages			28	127	76.49

B. Manner of Reckoning Longevity

The date of arrival and the number of the specimens in each batch were recorded. Every day the cobra tenders inspected their charges and noted any deaths. The first death in a given batch is designated as cobra number one, the second, number two, and so on. The total number of days each survived (from the date of their arrival in the serpentarium) was recorded. When the last specimen in the batch died, the arithmetic mean longevity was determined. A total of 16 batches were involved in this study.

III. RESULTS AND DISCUSSIONS

Table I summarizes the results obtained in replicate experiments comparing the effects of the three schedules of venom extraction on the longevity of the cobras. The data collected in each case are expressed as the arithmetic average of all the respective observations. An inspection

of the averages shows a definite increase in longevity as the frequency of the extraction decreases.

The differences observed in longevity in experiments I, II, and III between groups 1 and 2 and between 1 and 3 were analyzed statistically and were found to be significant.

Figure 1 is a graphic interpretation of the data presented in Table I.

The results of the experiments to demonstrate the difference in longevity in two comparable groups of cobras—group I, from which venom was extracted fortnightly, and group II, from which no venom was extracted at all—are presented in Table II. The mean longevity obtained for group II is for practical purposes twice that obtained for group I.

Figure 2 gives a graphic picture of the combined data in Tables I and II. It clearly shows that venom extraction adversely affects longevity and

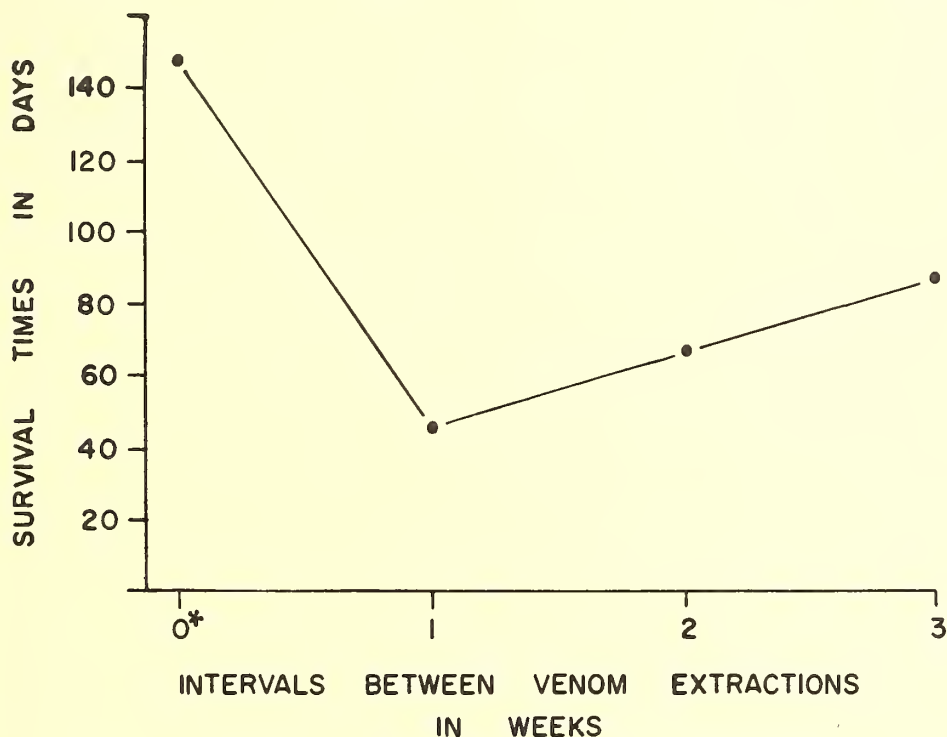


FIGURE 2 LONGEVITY OF COBRAS IN RELATION TO THE FREQUENCY OF VENOM EXTRACTION

* NO VENOM EXTRACTION

that the degree to which longevity is adversely affected is directly proportional to the frequency of venom extraction.

To better appreciate the monthly death rates and their trends and facilitate an interpretation on the basis of observations made, both in the serpentarium and in the fields during hunting trips, Figure 3 has been prepared. It gives the monthly mortality rate percentage computed on the basis of cumulative monthly populations and the cumulative monthly deaths covering a period of 43 consecutive months, January, 1960, to July, 1963.

In presenting the following interpretations of Figure 3 the possible source of error mentioned above has been kept in mind and only those supported by observations made both in the serpentarium and in field trips are made:

1. Considering that, generally, June to November is our rainy season and December to May our dry season, we have higher death rates during the "wet" than during the "dry" season. From the data obtained we get an over-all average death rate of 35.3% for the former and 19.3% for the latter. Death rates are lower during the cooler part of the "dry" season, December to February, than during the warmer part,

March to May, reaching a peak in the latter month.

2. The slump in death rate in June may be explained by the cooling effect of the first mild rains of late May and early June.

In the serpentarium the only protected spaces to which the cobras have access are the hollows of the cement blocks, which offer limited insulation to extremes of temperature and very little protection to drenching rains. The earliest rains experienced during late May offer relief from the usually scorching heat, which reaches a peak by May. This offers a logical explanation for the sudden drop in death rate noted. With more and heavier rains the earth becomes soggy, water becomes stagnant, and the hollow blocks are drenched. The skin of the snakes gets soaked and soft, making them, possibly, more vulnerable to systemic and skin diseases (as indicated by their noticeably rundown condition and dull roughened scales during this period). As the rainy season progresses there is noted a rise in mortality rate which reaches a peak in September.

3. As the rains abate toward the end of the "wet" season, a gradual decrease in the death rate is again noted.

Table III is a summary of the data on the

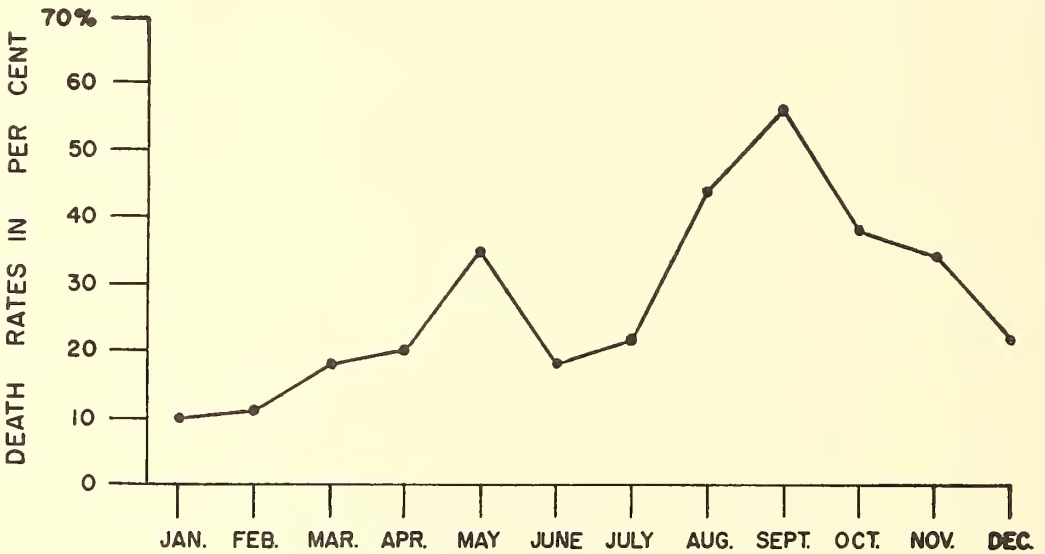


FIGURE 3 SHOWING THE TRENDS IN MONTHLY DEATH RATES

batches involved in this study, which were subjected to the uniform schedule of fortnightly venom extraction. From the data presented, there appears to be no relation between the month of the year the batches were acquired and the mean survival times of the respective batches.

IV. SUMMARY AND CONCLUSIONS

A total of 2,075 cobras were observed in the serpentarium of the SVL over a period of 43 months.

The data collected indicate that:

1. Longevity is adversely affected by the frequency of venom extraction; the more frequent the extraction, the shorter the span of life.

Under the conditions at the SVL serpentarium, cobras not subjected to venom extraction that served as controls lived an average of 149.14 days. Individual longevity ranged from 31 to 226 days.

Snakes from which venom was extracted once in 21 days lived an average of 89.08 days, or 61% as long as the controls. Those from which venom was extracted once every 14 days lived an average of 69.84 days, or 46% as long as the controls. Snakes from which venom was extracted every 7 days lived an average of 48.18 days, or 32% as long as the controls.

2. Monthly death rates computed on the basis of cumulative monthly population and the corresponding deaths over a period of 43 months indicate two peaks, the lesser peak occurring in May, or about the height of the dry season, and the greater peak in September, corresponding to about the height of the rainy season.

3. An over-all average longevity of 76.49 days

was obtained from the data on 1,804 specimens uniformly subjected to fortnightly venom extraction. Individual longevity ranged from 2 to 202 days.

4. The time (month) of the year a batch of specimens was collected does not appear to bear any direct relation to the mean survival time of that particular batch.

5. The severe rains increased monthly mortality rates more than the extreme heat experienced during the period of this study.

V. ACKNOWLEDGMENTS

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Combat and Its Ritualization in Fiddler Crabs (Ocypodidae) With Special Reference to *Uca rapax* (Smith)¹

JOCELYN CRANE

*New York Zoological Society,
New York, New York 10460*

(Text-figures 1-3; Plate I)

[This paper is a contribution from the William Beebe Tropical Research Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, West Indies. The station was founded in 1950 by the Zoological Society's Department of Tropical Research under the late Dr. Beebe's direction. It comprises 250 acres in the middle of the Northern Range, which includes large stretches of government forest reserves. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

[For further ecological details of meteorology and biotic zones see William Beebe, "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.," *Zoologica*, 1952, Vol. 37, No. 13, pp. 157-184.]

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I. INTRODUCTION

MALE fiddler crabs sometimes seize each other's large claws at the climax of a fight. Physical damage practically never occurs, although the stronger sometimes flings the weaker inches away or flips him altogether upside down. Almost all combats, however, stop short of a violent finish.

The work described in this contribution shows that most combats are so fully ritualized that the observer can detect no element of force. In these encounters the end activity is the rubbing or tapping of a correlated but different part of the opponent's claw. Morphological specializations include ridges, tubercles, and other structures with functions previously unknown.

At times the effective meeting of parts seems to be achieved through cooperative movements of the less-active crab. In the most elaborate combats the components are performed by each individual in turn, while his partner holds still.

Preliminary observations on ritualized combat in *Uca* were made in the Indo-Pacific (Crane, 1966). In some species the claws, partly engaged, vibrated back and forth with a clicking sound audible to the observer. Detailed descriptions were not secured in the field, although motion pictures recorded the pattern. In other forms, pits and tubercles apparently served as deterrents to forceful linkage of the chelipeds. These observations, made incidentally during a study of waving display, all showed the need for a concentrated study of combat.

The fieldwork described below was accordingly undertaken in Trinidad during 1966. A socially advanced neotropical species, *rapax*, was selected as the principal subject; comparative observations on other species have begun. The resulting contribution gives some basic information on the occurrence, organization, and results of combat and discusses its possible functions.

My thanks go to Pauline Thomas for Text-figures 1 and 3, to Julie C. Emsley for Text-figure 2, and to Kathleen Campbell for her aid in the laboratory and in reviewing film.

Headquarters for the study was the New York Zoological Society's William Beebe Tropical Research Station, Arima Valley, Trinidad, West Indies.

II. HISTORICAL REVIEW

The fighting proclivities of male fiddler crabs have long been familiar to naturalists and are even celebrated taxonomically in the species names *pugnax*, *pugilator*, and *bellator*. Compared with other conspicuous fiddler activities, however, combats are so uncommon, short, fast, and superficially similar that it is not entirely surprising that their patterned complexities have been overlooked. The infrequent reports have been only roughly descriptive and wholly unanalytical. Examples include Pearse (1912); Dembowski (1925); Verwey (1930); Crane (1958, 1966).

Intermale threat postures and movements in *Uca*, which certainly should be regarded as ritualized fighting, have been more fully reported, especially by Altevogt (1957), von Hagen (1962), and Schöne & Schöne (1963), in addition to the references just cited. This behavior is, however, arbitrarily excluded from the bounds of this contribution, where combat will be defined (p. 53) as any behavior between male *Uca* in which the claws of the chelipeds come into contact. For the same reason, references to waving display are excluded, although a great deal of waving is directed at other males and in many displays appears certainly to have developed in part from threat postures.

Intermale combat in other decapods occasionally has been reported but, again, only in general terms. It has been observed in other ocypodids, as follows: in *Dotilla*, by Tweedie (1954) and Altevogt (1957b); in *Heloccius* by Tweedie (1954); in both these genera as well as in *Scopimera*, *Macrophthalmus*, and *Ilyoplax* by Crane (unpubl.). Reese (1964), in a review of aggressive behavior in marine invertebrates, lists intermale ritualized combat as recorded in only three other genera of decapod crustaceans: the grapsid crab *Helice crassa*, observed by Beer (1959); another grapsid, *Pachygrapsus crassipes*, reported by Hiatt (1948), Bovbjerg (1960), and Schöne & Schöne (1963); and the goneplacid crab *Hemiplax hirtipes*, recorded by Beer (1959). Reese has not yet seen ritualized combat during his own investigations of pagurids although, as in a number of other decapods, intermale threat behavior and dominance relations occur.

Study of the acoustical behavior of *Uca* is now progressing (Salmon & Stout, 1962; Altevogt, 1962, 1964; von Hagen, 1962; Salmon, 1965; Crane, 1966), but the sounds of combat, which are occasionally audible to man, have yet to be examined. No tape recordings were made during the present study, although the above references form part of its background. The re-

view by Guinot-Dumortier & Dumortier (1960) on the morphology of stridulation in crabs gives no examples where one crab is presumed to stridulate against part of another individual.

A survey of ritualization in animals—in the sense used first by Huxley (1914) and developed especially by Lorenz (1941), Baerends (1950), and Tinbergen (1952)—is included in Huxley *et al.* (1966). Ritualized combat is specifically discussed by Lorenz (1964, 1966a, 1966b).

III. MATERIALS, METHODS, AND DEFINITIONS

Unlike the casual observation of fiddler combat, its ethological study is slow and inconvenient. Not only does combat occur uncommonly, but its characteristics are often difficult both to determine and to record for a number of reasons.

First, the physical conditions under which combat is prevalent are stringent. At least in the tropics, combat seems frequent only near new and full moon, around the time of a diurnal low tide, and during the optimum hours of waving display for the species (Crane, 1958, p. 117). The correlation of prevalence of combat with the moon is, it seems at present, closer than that of waving; the closer connection may, however, be more apparent than real because of the rarity of combats compared with the frequency of waving and of threat postures. As with waving, combats are more frequent in sunshine than in cloudy weather, other conditions being equal.

A second difficulty lies in the fact that numerous combats are instigated by aggressive wanderers (*loc. cit.* p. 119; present contribution, p. 53). It is now clear that these examples are very often irregular. In working out the normal patterns, therefore, it is important both to see their beginnings and to observe the subsequent behavior of each crab long enough to determine whether an aggressive wanderer is one of the protagonists. This ideal procedure is often impossible in practice because combats usually start unpredictably and because afterward it is frequently difficult to keep watch on two crabs, one of which is moving rapidly away through a crowded population.

Third, details of activities involving the crucial inner surface of the manus are invisible in many encounters, even when the observer sits within inches of the combat.

Fourth, since most encounters start without warning and end after a few seconds, filming and acoustical recording are difficult.

There seem to be no short cuts to winning knowledge of the patterns. Until their occur-

rence and outlines were established in the field, it appeared unwise to depend on observations made in outdoor terraria and in the laboratory.

Preliminary attempts here and elsewhere to record the sounds of high-intensity fighting have not yet been successful. Both aerial and contact microphones have been used. Little time has so far been spent on this aspect of the work, however, since the basic activity patterns first had to be determined.

The data in this paper, therefore, are based wholly on fieldwork undertaken in Trinidad during the summer and fall of 1966 and on a review of motion pictures photographed on earlier trips to the Indo-Pacific and tropical America. The method of study was observation, note taking, scoring with and without binoculars, and photography with a 16-mm. Eastman Cine-special camera equipped with a 150-mm. telephoto lens. Combats were timed with a stopwatch and by mentally counting off seconds; for details see p. 53, under "Duration."

Most of the observations were made on *Uca rapax* (Smith), with comparative work on *U. cumulanta* Crane. These species were studied chiefly near the mouth of the Diego Martin River, west of Port-of-Spain. Active populations were selected in undisturbed areas.

All of the counts were made on a small plateau on the left bank of the river. Roughly circular, this area was about 15 feet in diameter. The terrain was typical for displaying populations of *rapax*—sandy mud that, although bare of vegetation, was adjacent to grasses and mangroves. The principal inhabitants were mature individuals of *rapax* and *cumulanta*; at optimum hours the great majority of males of both species displayed. *U. rapax* was more abundant on the top of the plateau, *cumulanta* on the damper, sloping sides, closer to the river and a tributary stream. The adjacent low ground supported flourishing populations of both species that were wholly without displaying individuals.

The portion of the plateau under observation was an arc of 120° with an average radius of 7 feet. About 75 to 100 *rapax* males displayed within this arc at any one moment during optimum display conditions. Three to five aggressive wanderers were usually active daily on the entire plateau, with one or two usually within the observation arc. To locate and count combats the arc was scanned without binoculars, by a single swing of the head averaging about 20 seconds; the swing was repeated at once if no combat was seen. When a combat or the strong threat of one was located, scanning ceased until all observational data possible had been noted from it, with or without binoculars.

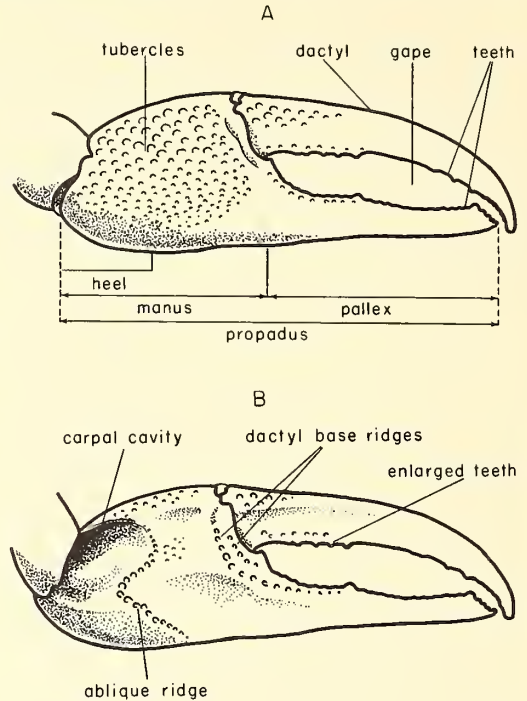
The descriptions and counts in the following pages are based on 337 of these combats observed in sufficient detail to give information on one or more of the topics examined. Except where noted in the headings, therefore, the same combats were not necessarily included in all the tables or in the counts and percentages given in the text. The periods of observation totaled 30.5 hours under favorable lunar, tidal, and daylight conditions, distributed as follows during 1966: August 17-19 and 30-31; October 13-17; November 26-29. Excluded from these totals and dates are preliminary observations made before all the combat components were determined, along with their morphological specializations, their general sequence, and the existence of mutuality. Also excluded are combats occurring during an hour or more of observation under good conditions after every absence from the field, for example between the October and November sessions; for me this period of getting back into practice was an essential safeguard against false and incomplete observations. For similar reasons, no observations are counted that were incidentally made while photographing. Finally, combats are excluded that occurred during the first 15 minutes of every observation period; it appeared that this length of time, for this population of *rapax*, was more than enough for the crabs to become habituated to the observer's presence, so that their subsequent behavior was unaffected. (In disturbed populations and always when observing very large species a blind would be highly advisable for studies such as this.)

Tables I-VIII (pp. 55, 56, 60, and 64-67) show the number of observed examples of various kinds of combats and their components on which the accounts of *U. rapax* in the following pages are based.

Table IX (p. 69) lists species and numbers of combats filmed in previous years in which patterns were clear enough to give data now useful.

Text-figure 1 shows the location of the morphological parts of the male's large claw. A review of the terminology may be helpful to ethologists unfamiliar with crustaceans.

The **claw** consists of the two terminal segments of the heterogonically enlarged first leg of the male. This entire appendage is termed the **major cheliped**; in this paper, since the minor cheliped is not mentioned, the adjective "major" will be omitted except in a few cases of possible ambiguity. The segments of the claw are (1) the **propodus**, consisting of the **manus** and the **pollex** ("fixed finger" of some authors), an extension of its lower part; and (2) the **dactyl** ("movable finger"), which is attached to the upper distal portion of the manus. The dactyl and pollex together form the **chela**, the grasping part



TEXT-FIG. 1. *Uca rapax*. Claw of major cheliped, to show location of structures used in combat. A, outer view; B, inner view.

of the entire claw. The word **heel** is used for the outer lower proximal portion of the manus, while **gape** denotes the space between dactyl and pollex. On the upper inner part of the manus is the **carpal cavity**. **Tubercles** of importance occur on the outer manus, on **ridges** of the inner manus, and close to the gape. Those of concern in the present study are: (1) on **outer manus**: enlarged tubercles, on either the upper or lower part of the manus, depending on the species; (2) on **inner manus (palm)**: an oblique tuberculated ridge running from the proximal lower margin to the carpal cavity and sometimes continuing around the anterior margin of the cavity to the dorsal margin of the manus; (3) on **inner manus**: one or two tuberculated ridges, approximately vertical and roughly parallel to base of dactyl, the more proximal continuing ventrally in a curve around the base of the gape between dactyl and pollex and continuing for a way along the upper margin of the pollex; (4) on **pollex and dactyl**: submarginal tubercles and marginal **teeth** set along the gape, on the lower edge of the dactyl and upper of the pollex. Small tubercles or rugosities are often present on the upper proximal part of the dactyl.

Definitions of general terms are, for the purpose of this paper, as given below. Three considerations determined their selection. The first aim was to avoid misunderstanding in the use of words and phrases that are not always employed in the same way by all ethologists or that

for this contribution needed limitation; an example is the word "combat." The second aim was to define terms that might be unfamiliar to workers who are not ethologists. Finally, specific combat activities and associated activities, a number of which are recorded for the first time in this paper, are briefly defined in the list; fuller descriptions, in context, follow on the indicated pages. To facilitate reference, the entire list of terms is given alphabetically rather than in any topical order.

Actor—In *Uca* combat, the individual at the moment performing the movements of a component.

Afterlunge—Feint by a burrow holder directed toward departing opponent. This activity is often associated with combat. (P. 61.)

Aggressive wanderer—A male *Uca* in the phase described below.

Aggressive wandering phase—The crab moves apparently at random through a population that includes displaying males, punctuates his passage with threats toward them, engages them in combat, makes superficial burrow explorations, and attempts unsuccessfully to mate. This phase is preceded by one of nonaggressive wandering. In *rapax* it is followed directly by the display phase, a predisplay territorial phase being apparently absent. Instead, the aggressive wanderer begins his waving display as soon as he occupies a particular burrow. For further details see below, p. 62.

Burrow holder—Equivalent, in *rapax*, to a crab in the display phase, always visually characterized by waving (see below). Because of differences found in other parts of the genus in the relationship of territoriality to display, the term "territory" and its derivatives are avoided in this paper, except in discussing the few combats that took place between burrows. In *rapax* the burrow itself is almost always the focus of combat, yet because of the frequent development of ritualization into a goal activity, it seems that strongly territorial terms such as "burrow defender" should not be used, even though some combats would make them wholly appropriate. Individuals, including females, that are not in display phase often occupy a burrow indefinitely; since they never engage in combat and never display, however, they are not concerned in this contribution; a serviceable term for them would be "burrow occupants."

Combat—A general term for any behavior between male *Uca* in which the claws of the chelipeds come into contact. Because of the usually high degree of ritualization, it might be preferable to substitute the word "encounter," thus avoiding the "loaded" words "combat" and "fight." Since the behavior discussed undoubtedly has an aggressive base, frequently shows overtly forceful components, and probably often includes pushing elements effectively masked by the ritualizations, it seems permissible to use all three terms. In this paper, therefore, "combat" is selected for general use; "encounter" appears occasionally in the discussion of fully ritualized combats; and "fight" is restricted to combats with overtly forceful components.

Component—An activity that is a characteristic part of combat and appears to the observer to be distinct from adjacent actions.

The most clear-cut examples are so distinct and so stereotyped that they may confidently be termed fixed action patterns, in the sense developed by Lorenz and Tinbergen and now often used in ethological studies. These examples are characterized not only by distinctive motor patterns but by juxtaposition of specialized morphological structures. In all of them overt force appears to be absent and they are here considered completely ritualized.

Other activities, however, are far less stereotyped and show considerable variability connected neither with intensity nor with transition to other combat actions. All of these, instead, often appear instantly adaptable to the changing circumstances of a fight. All show overt use of force since the chelipeds are used variously as a pushing, grasping, and lifting organ. These activities are regarded as unritualized. Any or all may need subdivision or other modification. Only further study with emphasis on comparative work within the genus can resolve the uncertainties.

Therefore it seems that the use of "fixed action pattern" would be at present a semantic disservice. The more general word "component" is adopted instead, in the same spirit shown by morphological taxonomists when they feel it premature to use a definite term such as "subgenus" and compromise on the noncommittal "group."

Dactyl slide—In *rapax* a ritualized component in which one crab rubs his dactyl teeth along the upper edge of his opponent's dactyl. (P. 57.)

Display—Here confined to a rhythmic motion of the major cheliped, species specific within the genus; movements of other appendages often accompany it. Used interchangeably with "waving" and "waving display."

Display phase—The phase characterized by waving, burrow holding, threat, combat, and courtship. In *rapax* it is preceded by the aggressive wandering phase.

Downpush—One crab is pushed down his own burrow by his opponent. An activity associated with combat. (P. 61.)

Duration—Timing of a combat from the moment at which the two chelipeds come into contact to their separation immediately preceding the departure of one of the opponents. Associated activities, ranging from preliminary threat behavior to afterlunge, were not timed, either as part of the combat proper or separately. Because of the difficulties of observing closely certain other constituents of each combat—especially its start, the phases of the opponents, their relative sizes, and their subsequent behavior—accurate timing with a stopwatch finally was discarded as a relatively expendable activity. Instead, counting seconds mentally was substituted, as in photography. Periodic checks with the stopwatch showed this system to be fully accurate within the broad limits of the two periods that turned out to be important to this study. During

future fieldwork it will be feasible, now that the basic work has been completed, to concentrate adequately on duration, both of combats themselves and of associated activities. As will be seen from the discussion, such records now become imperative.

Encounter—Fully ritualized combat. (See also **combat**.)

Fight—Combat including forceful components. (See also **combat**.)

Fling—A variable, unritualized component at the close of a forceful ending. One opponent is pushed backward in a skid or is partly overturned. (P. 59.)

Forceful component—In low-intensity combat—manus pushes; in high-intensity combat—grips, flings, and upsets. All are highly variable and seem to be entirely unritualized, since the cheliped is used variously in pushing, grasping, and lifting.

Forceful end—Unritualized behavior at the end of a high-intensity fight, consisting of a grip by one opponent and sometimes followed by a fling or by the total upset of the other crab.

Grip—A forceful component consisting of the seizure by one opponent of the other's claw. (P. 59.)

Heel-and-ridge—A high-intensity ritualized component in which the actor places his dactyl outside the manus of his opponent while the pollex passes to the inner side, the palm, and rubs its oblique ridge. (P. 57.)

Heteroclaved combat—In one opponent the claw on the right side is enlarged, the other on the left.

High-intensity combat—Part of the claw of each opponent comes between the dactyl and pollex of the other. In forceful endings the claw tips may grip the opponent's claw; in fully ritualized encounters they do not do so. In *rapax* the available components consist of dactyl slides, heel-and-ridges, and interlaces; a low-intensity component, the manus rub, often initiates high-intensity combat.

Homoclaved combat—Both opponents have the claw of the same side, either right or left, enlarged.

Instigator—In combats between two burrow holders, the crab that approaches his future opponent; except for this approach, he does not necessarily ever become an actor. In combats between an aggressive wanderer and a burrow holder, the wanderer is always the instigator. Because of the usual high degree of ritualization, the words "aggressor" and "attacker" are not used.

Interlace—A ritualized component prevalent in heteroclaved combat. With the bases of both chelae almost in contact, proximal claw teeth on one crab rub against a distal manus ridge of the opponent. (P. 58.)

Left-clawed—Cheliped on left side enlarged.

Low-intensity combat—Contact is confined to the outer surfaces of the mani and chelae. In *rapax* the components consist of the forceful manus push and the ritualized manus rub. (P. 57.)

Manus push—See **Low-intensity combat**.

Manus rub—See **Low-intensity combat**.

Mero-suborbital friction—The rugosities on the upper merus of the cheliped are rubbed against the outer crenulations of the lower margin of the adjacent orbit. Behavior associated with combat. (P. 61.)

Mutual combat; mutual components—Both crabs perform one or more of the components, either in sequence or alternately. They can perform simultaneously only during manus rubs. (P. 63.)

Phase—A temporary condition of *Uca* characterized by one of a number of general behavior patterns. These have already been described (Crane, 1958). Of concern in this paper are the aggressive wandering and display phases, defined above. The term "phase" is retained here in preference to its possible alternate, "state," because the latter is often used in work with other animals for conditions controlled by long-term endocrine activity. At least in the tropics phases appear regularly to last only hours or days. The causes of phases remain uninvestigated.

Right-clawed—Cheliped of right side enlarged.

Ritualization—Any short definition or description of ritualization in animals must be inadequate. Furthermore, not all workers in ethology agree on the boundaries of ritualization or, rarely, even on the need for the concept. To me, however, much of the social behavior in *Uca* would be unintelligible without it. It is hoped that the following paragraphs may serve as a frame of reference for the present study of combat. Key contributions, classical and recent, on ritualization include Huxley (1914, p. 491; 1966, pp. 249–271), Lorenz (1941, 1964, 1966a, 1966b), Baerends (1950), Tinbergen (1952, 1953), Blest (1961), Hinde (1966, p. 432) and Thorpe (1966).

In animal behavior ritualization is an evolutionary process whereby social patterns develop partly through transformations of movements and structures that originally functioned during other activities. For example, a bird's courtship display movements may include recognizable traces of feeding and preening behavior. In the course of evolution both the motions and the associated morphological characteristics become simplified, exaggerated, or both. These changes often make a visual display, for instance, conspicuous, unambiguous, and distinct from that of related species. In short, they produce an effective signal in communication.

In other cases, ritualization serves to reduce intra-specific damage in combats between males. Here ceremonial encounters replace injury-producing use of weapons, while the advantages of aggression are maintained. The ritualized motions are often intention movements of actual fighting, more or less transformed and often, as in display, emphasized by the enhancement of associated structures. Also, as in display, parts of sequences from other contexts may be altered and included. Sometimes these combats are token tests of strength, and damage is avoided at the climax by stereotyped signals of pos-

ture and motions. Sometimes force seems wholly to be absent. Although ritualization in *Uca* combat obviously belongs in this general category, both its origins and its functions remain obscure, awaiting comparative study within the genus. They are briefly discussed, beginning on p. 72.

Ritualized combat—Encounters without forceful components.

Ritualized components—In *rapax* these include manus rubs, dactyl slides, heel-and-ridges, and interlaces. No pushing, grasping, or lifting motions are included.

Tapping—At the end of a ritualized component the teeth of the dactyl or the pollex or both tap against part of the opponent's dactyl or manus. (P. 59.)

Territorial phase—See **Burrow holder**.

Threat—Aggressive postures or motions confined, in male *Uca*, to individuals in the aggressive wandering, territorial, and display phases. Although threats usually precede combat, they occur far more often than combats. As in other animals they should be considered as classic examples of ritualized combat. Already described briefly and illustrated elsewhere (*ibid.*, 1958, p. 123; 1966, p. 464), they are arbitrarily excluded from this contribution through the selected definition of "combat." They will be further examined in a subsequent publication on the comparative ethology of combat behavior.

Upset—Unritualized, final component, where one crab is turned completely upside down. The rarest of all components. (P. 59.)

Wanderer—In the present paper used only for "aggressive wanderer," and then only where the latter term has already appeared in the same paragraph.

Wandering phase—In *Uca* a nonaggressive phase, characterized by lack of attachment to a particular burrow. It precedes the aggressive wandering phase

(*ibid.*, 1958, p. 119). Not concerned in the present paper.

Waving; Waving display—See **Display**.

Withdrawal—Behavior associated with combat, where a burrow holder goes partway or entirely down his own hole. (P. 60.)

IV. COMBAT IN *Uca rapax*

A. Relevant Characteristics of Opponents

The pattern of a combat between *rapax* males depends largely on three factors: the phase of each individual; the relative size of the two crabs; and the location—whether on the right or left side—of the large claw of each.

1. *Phase*—Males engage in combat only when they are in either the aggressive wandering phase or the waving display phase. In the latter condition they are always burrow holders. Combats take place only between an aggressive wanderer and a burrow holder or between two burrow holders; encounters between two aggressive wanderers are unknown. When a wanderer elicits combat from a burrow holder irregular components are frequent and a ritualized encounter sometimes ends as a forceful fight. In contrast, combats between neighboring males are usually composed of highly regular, ritualized components and practically never end in force. These categories and their results will be described beginning on p. 62.

2. *Relative size*—The larger crab in all combats usually has the advantage. It is interesting, therefore, that in the majority of combats including an aggressive wanderer, the latter instigates combat with a burrow holder larger than he. See Table I.

TABLE I.
Uca rapax. RELATIVE SIZES OF OPPONENTS IN COMBATS WHERE INSTIGATOR WAS DETERMINED.
(Based on a total of 151 combats. Locality and dates as in Table II.)

Aggressive Wanderer vs. Burrow Holder		
Aggressive wanderer (always instigator) larger.....	22	
Aggressive wanderer smaller	66	
Aggressive wanderer & burrow holder about equal.....	6	
Total	94	94
Burrow Holder vs. Burrow Holder		
Instigator larger	36	
Instigator smaller	17	
Opponents about equal	4	
Total	57	57
Grand total		151

3. *Claw of same or opposite side enlarged*—In *rapax* right- and left-clawed individuals occurred in equal numbers in two population samples (unpubl.). In Maracaibo, Venezuela, the sample totaled 186; in the Trinidad study area, 252. Tables II and III show no tendency in combat for instigators to approach opponents

having the same claw enlarged as their own rather than the claw on the opposite side. Therefore, homoclawed and heteroclawed combats are about equally likely to take place. Table III shows clearly that the frequency of several of the components described below is affected by this characteristic.

TABLE II.

Uca rapax. COMPOSITION OF 154 COMBATS OBSERVED AT COCORITE, TRINIDAD, OCTOBER 13-17 AND NOVEMBER 26-29, 1966.

(Note: Combats are listed only if observation is believed to have included the first component.)

Sequences of Components	Combats Between an Aggressive Wanderer and a Burrow Holder		Combats Between Two Burrow Holders		Total
	Homo-clawed	Hetero-clawed	Homo-clawed	Hetero-clawed	
Manus push only	1	..	1	1	3
Manus push + manus rub	2	2	4
Manus rub only	19	10	18	10	57
Manus rub + dactyl slide	1	13	3	6	23
Dactyl slide only	1	3	1	1	6
Manus rub + dactyl slide + heel-and-ridge	1	1*	1	..	3
Manus push + manus rub + heel-and-ridge	1	..	1
Manus rub + heel-and-ridge	9**†	4*	4	2	19
Dactyl slide + heel-and-ridge	1	..	1	1*	3
Heel-and-ridge only	5*†	..	5**	1	11
Manus rub + interlace	..	5†	5
Heel-and-ridge + interlace	..	4	4
Interlace only	..	2†	..	2	4
Manus rub + heel-and-ridge + interlace	1	1
Dactyl slide + heel-and-ridge + interlace	..	1†	1
Manus rub + dactyl slide + heel-and-ridge + interlace	..	3†	..	1	4
Manus rub + dactyl slide + interlace	..	2	..	1	3
Dactyl slide + interlace	1	1	2
Total	40	49	37	28	154

* 1 heel-and-ridge component not followed by tapping.

** 2 heel-and-ridge components not followed by tapping.

† 1 combat with forceful ending included.

TABLE III.

Uca rapax. RELATIVE FREQUENCY OF COMPONENTS IN 154 COMBATS. (From data in Table II.)

Component	Frequency (%)	
	In 77 homoclawed combats	In 77 heteroclawed combats
Manus push	6	4
Manus rub	78	77
Dactyl slide	14	44
Heel-and-ridge	38	23
Interlace	3	29

*B. Behavior Components and Their
Morphological Specializations
(Tables II and III)*

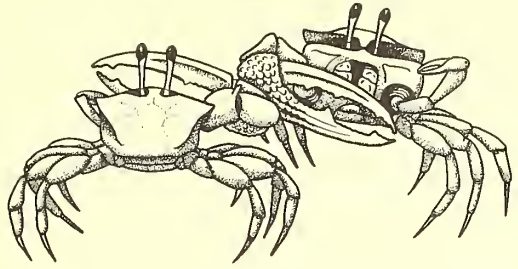
All combats are based on seven components. These are described below, in the order of their usual occurrence. Component 1 or 2 or both may form the entire combat; usually 2 precedes one or more additional elements. Components 1 and 2 are regarded as low-intensity components, and 3 through 6 comprise the highly ritualized, high-intensity components. The infrequent forceful grips and upsets are grouped under Component 7.

As shown in Table II, all the components never occur in a single combat. The sequence given below is altogether characteristic, but reversals of order among high-intensity components occasionally take place, particularly in long mutual combats. These reversals may or may not be followed by repetitions of previously performed components. The combat pattern, therefore, is not rigidly constructed of a fixed sequence of interdependent components. The omissions and irregularities are such that it does not seem wise to stylize the data so far assembled into a diagram of a "typical" combat sequence, or even into any kind of flow diagram. Instead, it is felt that tables present the complexities of the subject in a more realistic manner.

1. *Manus pushes*—The chelipeds are held flexed, the chelae partly open through slight lifting of the dactyls. Meanwhile the lower, smoother halves of the mani are pushed against each other. It often seems impossible to decide whether or not a manus push includes a rub component or vice versa, and the totals given in the tables are approximate.

2. *Manus rubs*—The same surfaces as in the manus push are rubbed back and forth, longitudinally, against each other. In *rapax* and related species the surfaces in contact are smooth, rather than coarsely tuberculated as in some other sections of the genus (Text-fig. 2). It is possible that the rubbing over the smooth surface facilitates the attainment of high-intensity components. At these times the manus rub continues past the bases of the gapes until the chelae are in contact externally and are free to proceed to one or more of the following positions.

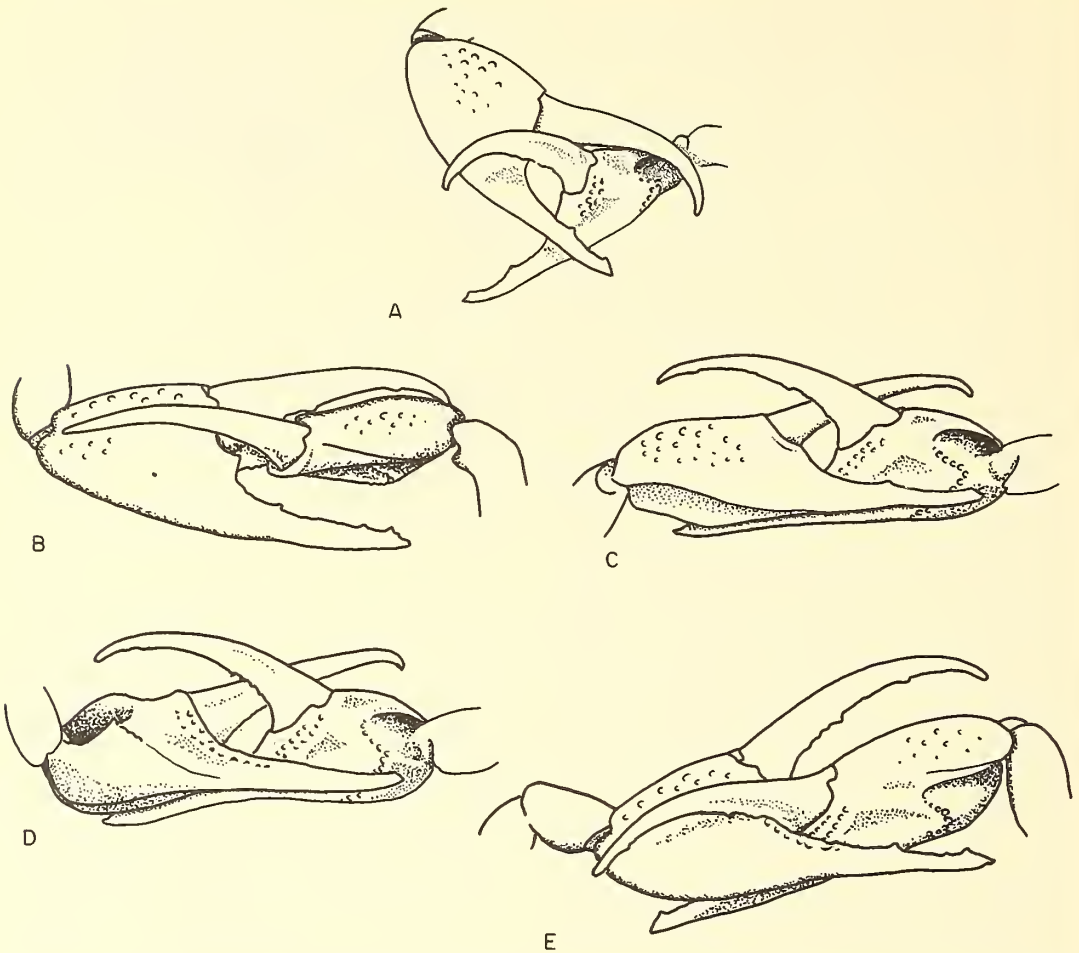
3. *Dactyl slides* (Text-fig. 3A)—With the chelae of both crabs partly open, the dactyl of one moves on top of that of the opponent, at about middle of its length, more or less at right angles, while the pollex passes within the gape. The approach may be from either the inner or the outer side of the claw. Both chelae are by then widely opened and the pollex does not



TEXT-FIG. 2. Low-intensity combat in *Uca*. Semi-diagrammatic view of position assumed by many species throughout the genus during manus pushing and rubbing. During homoclawed combat, as above, the manus of each opponent sometimes lies against the opponent's pollex. In heteroclawed examples the claws are usually lined up parallel, from manus heel to chelae tips. The dorsal margins of the mani are sometimes, as in the figure, at unequal heights, sometimes at the same level. See text, p. 57.

touch the opponent's fingers. Gentle maneuvering for this position may continue for several seconds. Once it is achieved, the rounded teeth of the actor's dactyl slide longitudinally back and forth along the smooth middle portion of the upper edge of the opponent's dactyl. No force seems to be used by either crab and no attempt is made to use the claws as pincers, all four tips being at all times free in the air. Except for the sliding motion both crabs remain almost motionless. An infrequent climax is the vibratory tapping of the uppermost dactyl against the one held quietly beneath it. In this species the vibration is performed only by the crab with the dactyl on top. Afterward the two crabs break suddenly apart. When tapping does not occur, the encounter either breaks off after at most several seconds of slide or, infrequently, passes into Component 4 or 5 below. Dactyl slides occur more often in heteroclawed than in homoclawed combat.

4. *Heel-and-ridges* (Text-figs. 3B, 3C; Pl. I, Figs. 1, 2.)—In *rapax* and many other species the dactyl, longer than the pollex, curves downward beyond it. This characteristic proves to be of definite use in heel-and-ridging, where the dactyl arches around the curving heel outside the manus of the opponent. On its way toward the heel, the dactyl tip appears to feel its way, using as a guide the outer crease along the base of the dorsal marginal ridge. Afterward, upon reaching the proximal part of the manus, the dactyl tip does not touch the heel except during the climax to be described. Meanwhile the pollex, shorter than the dactyl and virtually straight, comes into contact with the oblique tubercu-



TEXT-FIG. 3. High-intensity combat in *Uca rapax*. A, dactyl slide; B and C, heel-and-ridge with tapping in homoclaved encounter; D and E, interlace in two forms of encounter. In B the crab on the left is the actor, his dactyl tip touching his opponent's heel; in C the same actor's pollex on a reverse stroke is hitting the opponent's oblique ridge, his dactyl tip being now separated from the heel; the same pollex position is used during the rubbing of the oblique ridge during the earlier part of the component. The interlace shown in D illustrates the more usual, heteroclaved form of this component; the right-clawed crab on the right is the actor, getting into position to bring dactyl teeth against opponent's ridge along inner base of dactyl; see also Pl. I, Figs. 3 and 4. E shows the interlace in its less common form, in homoclaved combat; the crab on the right is the actor, rubbing basal teeth of dactyl against basal teeth and outer tubercles of opponent's pollex. See text, p. 57 ff.

lated ridge of the inner manus. The pollex teeth, in the seven examples where an adequate view or film was secured, rub up and down along the oblique ridge. At the climax, however, the actor taps the ridge rapidly three or four times with his pollex; on opposite strokes, when the pollex is away from the ridge, the teeth near the dactyl tip come into contact with the manus heel. At highest intensity the tapping is faster and of smaller amplitude; the effect is vibratory (p. 59). When crabs are not closely matched in size, the parts coincide poorly and it is the acting crab—

not necessarily by now the original instigator—that performs the tapping. No attempt at seizing and gripping has ever been detected when the claws are in the heel-and-ridge position. A heel-and-ridge, with or without tapping, may be preceded by a manus rub or infrequently by a dactyl slide. Occasionally in mutual, heteroclaved combat a heel-and-ridge is followed by or alternates with an interlace.

5. *Interlaces* (Text-figs. 3D, 3E; Pl. I, Figs. 3, 4.)—In this component the fingers of each claw overlap the opponent's manus, so that the

bases of the gapes are almost or wholly in contact. The sequence is characteristic of heteroclawed combats although not confined to them. Typically the position is assumed by the crab that has its dactyl against the inner side of the opponent's manus rather than against the outer side, which is the position for a heel-and-ridge. In a fully developed interlace the chela of each crab is wide open through high elevation of the dactyl; the tips of both pollex and dactyl are wholly free from contact with any part of the opponent. In this position the most proximal teeth of the pollex come into contact with one or both of the tuberculated ridges paralleling the base of the opponent's dactyl and rub up and down along their course. At highest intensity the rub follows along the longer, less-variable subdistal ridge that continues from the dactyl base down around the base of the gape and out along the proximal, upper, inner portion of the pollex.

The climax usually consists of frication by the pollex teeth as just described, whereupon the encounter ends. This component may culminate in serial taps similar to those following a normal heel-and-ridge component but made, instead, by the basal gape teeth against the subdistal ridge of the manus in the interlace position. While a tapping finale is the normal end of a fully developed heel-and-ridge component, it is uncommon after an interlace and, as when it follows a dactyl slide, cannot be regarded as typical (p. 57).

An interlace is usually preceded by a manus rub and less often by a dactyl slide. It also occurs in mutual heteroclawed encounters when one opponent, with the dactyl against the inner side of the other's manus, performs the interlace. Usually it is the temporarily more active crab, in passing from a low-intensity manus rub to high-intensity, that assumes the heel-and-ridge position, with the dactyl outside the manus; hence the second crab arrives automatically in a position appropriate for the interlace.

6. *Taps*—As already described, tapping occurs most frequently at the end of a heel-and-ridge component. Sometimes it is preceded by an interlace or dactyl slide; rarely by a manus rub. Always it consists of the rapid tapping of the dactyl or, in most heel-and-ridge sequences, of the dactyl and pollex alternately, against a particular part of the opponent's claw. Rather slow tapping of wide amplitude is performed both by aggressive wanderers and by burrow holders. Rapid taps of narrow amplitude are performed only by a burrow holder, usually at the end of an encounter beside his own hole. The several examples recorded on motion picture film appear

as blurs on frames exposed at 1/48 second. After tapping, a combat often breaks off abruptly.

7. *Grips, flings, and upsets*—In contrast to Components 2 through 6, the occasional forceful end of a combat is composed of irregular elements that appear to be largely or wholly unritualized. They may be grouped under grips, flings, and upsets—descriptive terms for actions that merge into one another.

A grip occasionally follows an unsuccessful attempt by an aggressive wanderer to get into the heel-and-ridge position; the fingers then slip beyond the normal position and firmly seize the base of the manus with one finger hooked into the carpal cavity; even the carpus itself may be grasped. Sometimes grips occur when two crabs are grossly mismatched in size; then the larger may seize the entire manus of the smaller crosswise between his fingers. More often the forceful component consists only of a longitudinal grip, with perhaps an undetected push, the actor then opening his fingers. Almost always the crabs then separate.

The term "fling" here includes those actions, always starting with a grip, that result in a skid or partial upset of the opponent. The momentum of the actor's pushing grip carries the released crab sliding backward, or he is thrust off balance with some of his ambulatories off the ground. "Upset" is confined to actions resulting in the complete overturn of the opponent onto his carapace, with all of his ambulatories in the air.

Both the occurrence and the progress of these forceful endings have so far proved to be unpredictable. The following figures are relevant. In 180 combats in which the endings were adequately observed, 15 (8.3%) ended forcefully (6 of these are included in the group of 154 combats analyzed in Table II and are so indicated). In 14 fights the opponents were an aggressive wanderer and a burrow holder; the wanderer was larger than the burrow holder in 7 combats, smaller in 6, while his identity was uncertain in 1; homoclawed and heteroclawed combats were equally divided. In 6 fights the forceful component consisted of a grip only, 5 others ended in flings, and only 3 in total upsets. The burrow holder was the actor both during the preceding ritualized component and in the grip and subsequent action in 7 combats, the aggressive wanderer in 2, 1 of them resulting in the eviction of the burrow holder; in 2 fights both ritualized and force components were mutual, 1 of them resulting in the second observed eviction of a burrow holder; in 1 fight the action consisted wholly in the eviction of an aggressive wanderer that had slipped in while

the burrow holder was engaged with a neighbor. The ritualized components immediately preceding forceful endings were interlaces in 7 fights and well-developed heel-and-ridges with taps in 3; antecedents to the grip in the remaining examples were irregular or improperly observed. Finally, 5 fights were followed by reduced aggressiveness of the wanderer and 2 by the dispossession of a burrow holder by a wanderer.

The single forceful ending to a combat between burrow holders was very short; the slightly smaller instigator lightly seized the opponent's entire palm then released it and went home; both crabs promptly resumed waving.

In brief, about 1 in 12 combats had a forceful ending, usually consisting only of a brief grasp by one crab of the other's manus; 14 out of 15 fights were between an aggressive wanderer and a burrow holder; in most the burrow holder was the active crab at the end of the fight, seizing the wanderer and administering the final push, fling, or upset. Forceful components preceded reductions in the wanderer's aggressiveness in 5 combats and preceded the taking over of his opponent's burrow in 2. These changes in behavior will be further discussed beginning on p. 66 and are included in Table VIII.

C. Associated Activities

1. *Withdrawals*—Of the 154 combats observed most completely, one quarter included some degree of withdrawal by the noninstigating crab into his own burrow. These withdrawals are subdivided in Table IV, but the degrees indi-

cated form unsatisfactory comparison material.

As shown in Table I, in the majority of combats between aggressive wanderers and burrow holders, the wanderer, always the instigator, is usually smaller than the burrow holder. Conversely, in encounters between burrow holders, the instigator, which usually starts the combat at the mouth of his opponent's burrow, is most often the larger crab.

Withdrawal of an approached crab, it seems, would be a more likely action by a crab smaller than his opponent than by one larger than the instigator. It would be expected, therefore, that in combats involving wanderers there would be little withdrawal underground, since most wanderers are smaller than the burrow holders they approach. In contrast it would seem predictable that since burrow holders are usually engaged by larger burrow-holding neighbors, withdrawals among the first would be more numerous.

In the material at hand as shown in Table IV such differences are not apparent. Withdrawals of burrow holders in combat with aggressive wanderers are more numerous than those between burrow holders. A principal reason is that the figures for partial withdrawals in Column 3 are misleading elements in the totals. They are misleading because partial withdrawals are not often functional withdrawals from combat. In these cases the burrow holder instead clearly uses the upper part of his burrow as a firm foothold for the prosecution of the encounter. In the samples given in the table, as well as in a

TABLE IV.

Uca rapax. COMBATS INCLUDING WITHDRAWAL OF THE NONINSTIGATING CRAB INTO HIS OWN BURROW.
(Based on a total of 154 combats. Locality, dates, material as in Table II, p. 56.)

Key: AW..... Aggressive wanderer
BH..... Burrow holder

1 Type of Combat	2 Relative Size of Crabs	3 Degree of Withdrawal of Noninstigator			6 Crab wholly underground	Total
		Major side appendages above ground	Claw alone left Manus and chela flat on surface	above ground Chela tip vertical in air		
AW & BH	AW larger	3	3	1	5	12
	AW smaller	6	2	0	2	10
BH & BH	Instigator larger	5	0	3	7	15
	Instigator smaller	1	0	0	0	1
Total		15	5	4	14	38

number of other combats witnessed too incompletely to be included, I have seen these half-withdrawn burrow holders engage most effectively in all classes of combat. These engagements ranged from the most unritualized and violent upset of a wanderer to the delicate mutual frictions of well-matched neighbors.

Column 4 in the table is almost equally unsatisfactory, giving no indications of the prevalence of examples where the manus and chela are laid flat on the surface. Almost always this behavior is shown by a burrow holder that does not engage at all in combat with an approaching aggressive wanderer but simply withdraws below ground before the wanderer can touch him, leaving the manus and chela in sight. Hence the behavior properly belongs under the general heading of threat rather than of combat as defined here, and so is beyond the scope of this paper. The wanderer may or may not make prying motions at the claw with his own chela or ambulatories, or may even stamp on it before passing on. Only twice have I seen this type of withdrawal during an encounter where both opponents may have been burrow holders; these are not included in the table since they occurred in combats where the phase of the instigator was not certainly determined.

These flat-clawed partial withdrawals from aggressive wanderers have been observed often in other species. In all, they seem to occur principally in crowded populations. Unfortunately counts and distance measurements have not even been begun.

Where the chela tip appears vertically above ground (Column 5), it seems probable that the projecting tip represents a different degree of withdrawal mood in the retired crab.

Withdrawal wholly underground (Column 6) almost always occurs when the crab's opponent, whether aggressive wanderer or instigating neighbor, is larger than he.

2. *Mero-suborbital friction*—In two of the encounters between burrow holders in which the noninstigator withdrew, his opponent reached briefly down into the burrow with his small claw. The merus of the major cheliped meanwhile rubbed three to four times against the enlarged outer crenulations on the lower margin of his orbit. I have also twice seen the motion performed by *rapax* when wanderers reached down occupied burrows with the legs of the side opposite the large claw and, in the Indo-Pacific, by *U. vocans* (Herbst) in threat behavior when both opponents were on the surface.

3. *Downpushes*—In four examples observed in detail a crab actively pushed his opponent

down the latter's own burrow. Three of the combats were between burrow holders, the actor using the low-intensity manus push. In one of these the instigator was the smaller crab; the larger pushed him back to his own burrow, alternating manus pushes with manus rubs. The fourth downpush marked the end of a meeting between an aggressive wanderer and a burrow holder; the downpush was the only noteworthy part of the brief combat, which included a manus rub and an irregular interlace. In this fight the downpush was delivered by a final grip.

4. *Removal of burrow intruders*—Three times when a burrow holder returned to his hole after a combat nearby a third crab was in possession. On two of these occasions the returning crab dug the intruder out. On the third, the burrow holder, which was much the larger crab, thrust his major cheliped down the hole and flipped the smaller out; the action was too rapid for me to note details. In no case was the incident followed by any of the components of regular combat.

5. *Digging or prying out of opponent*—Only once was a digging or prying out motion observed during a regular combat. Here an aggressive wanderer had engaged a slightly larger burrow holder. At the end of an encounter composed of a manus rub, dactyl slide, and heel-and-ridge without tap, the burrow holder slid slowly down his hole. The wanderer disengaged, tried briefly to dig the other out with his major cheliped, and then departed.

6. *Afterlunges*—The term "afterlunge" is given here to an action frequently associated with combat, although the same or very similar behavior sometimes occurs in purely threat situations. With the cheliped more or less flexed, the crab lunges toward the opponent—either potential or recent. When associated with combat, an afterlunge always follows the encounter, sometimes so closely that perhaps it should then be considered a component. Such distinctions between afterlunges, however, would be too blurred to be practical.

The afterlunge was counted in 54, or almost half, of the 112 combats of all kinds in which its presence or absence was noted. It was almost always performed by the larger crab, and, except in boundary encounters, occurred at the mouth of his own burrow. Usually it followed a combat between an aggressive wanderer and a larger burrow holder—that is, the most frequent kind of encounter; 65% of all afterlunges followed such an engagement. Afterlunges were also common after boundary combats between burrow holders; one occurred, always per-

formed by a single crab, in 9 out of the 12 fully observed boundary encounters; in 7 of these examples the larger crab was the actor.

Particularly in combats including an aggressive wanderer, the burrow holder sometimes lunged just as the two crabs were separating and through this movement may even have brought about the wanderer's departure; these examples added an element of virtual force to an otherwise wholly ritualized and often mutual encounter. More often the burrow holder did not lunge until the wanderer, or instigating neighbor, was already at a distance. Once a small, instigating, burrow holder atypically lunged toward his former opponent after his return to his own burrow. Finally, after one of two forceful burrow seizures, the former aggressive wanderer waved and then lunged toward the dispossessed crab, which was circling about in the low posture characteristic of nonaggressive and nondisplaying *Uca*. This unusual example was the only combat seen where an afterlunge followed a forceful ending.

D. Categories

The preceding accounts of behavior components have mentioned two general classes of combats, those between an aggressive wanderer and a burrow holder and those between two burrow holders. The characteristics of each will now be considered as a basis for a review of combat results. Mutual combat occurs in both categories but will be examined more closely under subheading 3 below.

1. *Combats between an aggressive wanderer and a burrow holder*—These combats are notable for their irregularity, for the prevalence of forceful grips, and for the frequent withdrawal of a vigorous burrow holder from an encounter. In first determining the combat repertory of any species of *Uca*, in fact, it is misleading to concentrate on combats involving aggressive wanderers. Such descriptions might easily be as inaccurate as reports on the nest-building behavior of birds drawn from observations of individuals that have not fully reached breeding condition.

Unfortunately for the observer, the combat activities of fiddler crabs in this phase are often more numerous and certainly more easily foreseen than are encounters between burrow holders. It is temptingly convenient to select for attention an active aggressive wanderer and watch him on his progress through the population. Such a course is usually conveniently marked by the threats of burrow holders on his route. If his aggressive phase is well established, a number of combats may be thus observed. Once the

repertory of a species is partially known, of course, the combats instigated by these wanderers form a rich source of information.

The combats may be composed of one or most of the components previously described. Often, however, the high-intensity components—dactyl slides, heel-and-ridges, and interlaces—are imperfectly attained or the motions are atypical; tapping, if any, is of wide amplitude.

For example, several aggressive wanderers, after an uneventful manus rub, inserted both pollex and dactyl through the gape of the burrow holder's chela, instead of inserting only the pollex. No regular combat development by the wanderer seemed possible from this position. One such contest ended with the burrow holder's opening his chela wide and freeing himself. In another the crabs broke apart after awkward shaking and shoving. After each of these encounters the wanderer departed.

Similarly, an apparently clumsy attempt is sometimes made by the wanderer to attain a dorsal slide position. This the opponent thwarts by raising his own dactyl high. The maneuver does not happen in fully ritualized fights between burrow holders, when the opponent usually appears wholly unresisting and—one is tempted to say—cooperative. When a slide position is obtained, the wanderer sometimes saws back and forth transversely across a single spot on the opponent's upper dactyl rather than in the normal longitudinal direction.

The behavior of a burrow holder approached by an aggressive wanderer is often atypical of his normally aggressive display phase; this is true even when, as is usually the case, the wanderer is the smaller crab (Table I). As described under "Withdrawals" (p. 60), the burrow holder sometimes goes completely underground either when approached or later in the course of the encounters; sometimes he leaves the manus and chela, bent at the carpus, flat on the ground as in *maracoani* (Crane, 1958, Text-fig. 2). When the wanderer has passed, the burrow holder emerges promptly and resumes display.

All except one of the 15 forceful endings took place at the close of a burrow holder's fight with an aggressive wanderer.

2. *Combats between two burrow holders*—These encounters usually occur at the mouth of the burrow of one of the participants. In contrast to the usual procedure in combats started by an aggressive wanderer, the instigator in this category is usually the larger crab. A minority of encounters between burrow holders take place on or close to the boundary between two territories.

The same two neighboring crabs occasionally

proceed through highly ritualized combats a number of times during a single low tide. Sometimes a burrow holder seems to be attracted to his neighbor's vicinity by a combat between the neighbor and another crab, usually an aggressive wanderer. Irregularities in the performance of the components are rare, combats brief, and forceful endings practically absent.

3. *Mutual combats*—About one-third of all combats are strongly mutual in the sense that each crab performs at least one of the ritualized components. In the 154 combats analyzed in Tables II and III, mutual elements were detected in 38% of the combats between an aggressive wanderer and a burrow holder, and in 31% of those between two burrow holders. In 87% of the mutual combats including an aggressive wanderer, the latter was smaller than the burrow holder he approached; this figure is higher than the proportion (67%) of smaller wanderers in the entire combat sample (Table I).

In a few additional combats, which are included in Tables V and VI, an aggressive wanderer's only activity appeared to be the initial approach to the burrow holder. After that the burrow holder seemed to be the sole actor and the wanderer eventually departed. Similar cases were observed twice in combats between burrow holders. No doubt many more such examples were seen than are cited in the tables; they are not included since the instigator's inactivity, whether he was a wanderer or a neighbor, could be only suspected because the angle of observation was unsatisfactory.

The heart of the problem of instigator inactivity lies in the observation of low-intensity components, the manus rubs. The actor or actors are especially difficult to detect, even in motion picture close-ups, because manus rubbing is the only component in which mutual action can be performed simultaneously by both crabs; this of course is because the necessary juxtaposition of parts—outer manus to outer manus—is much less precise than in the subsequent components of high-intensity combat. Even in the analyses of highly mutual combats the counts for mutual manus rubs are doubtless low; when uncertain about the mutuality of a rub, I counted it as absent.

In ritualized components of high intensity—dactyl slides, heel-and-ridges, and interlaces—the actors either perform the slide in turn or exchange roles, the former actor holding still while the second crab performs the next component. Any necessary shift in position is made, including those demanded by a different size of claw. Sometimes the temporarily inactive crab is not only quiescent during and after the shift but

even appears to take a cooperative part in it. For example, after a slide a retiring actor brought his dactyl below that of his opponent, into the latter's gape, and then stopped moving. This left the other crab in the actor's position for the slide that promptly followed.

In mutual heteroclaved combats the heel-and-ridge is performed by the individual having his dactyl outside the manus, the interlace by the crab with the dactyl against the inner surface, as described on p. 63. When the second crab becomes the actor, he needs only to engage the claws farther, to the gape base, to attain fully the interlace position.

Only two examples of this type of heteroclaved mutuality appear in Tables V and VI, since these were the only such combats observed from their low-intensity beginnings, and for those tables it seemed best to include only fully observed examples. A total of 11 heteroclaved combats were in fact partially witnessed which included this alternate performance of heel-and-riding with interlacing; one record was secured on motion picture film; all except one of these additional examples took place between an aggressive wanderer and a burrow holder. Other mutual components recorded in the tables were also seen in greater numbers than indicated, but again observations were partial.

Although some mutual encounters were among the best examples of ritualized combat, with no discernible trace of force, in others aggressive elements were scarcely disguised. In these combats the shift from one actor to another was clearly accompanied by irregular pushing or by abruptly jerking motions of a claw in the midst of a component.

E. Duration

A total of 104 combats of all classes, each observed from its beginning, were approximately timed, as described on p. 53. The great majority turned out to be very short encounters, most of them lasting between about 3 and 8 seconds. The duration of a few ranged from 1 to 3 minutes. No records were obtained of complete combats lasting between 20 and 60 seconds; even the addition of incompletely observed examples, however, indicated that the combats of intermediate length were rare—rarer than the few of long duration. It seems likely that when sufficient data are accumulated the curve will have two peaks.

Relevant subdivisions are given in Table VII. Of the 104 combats timed, 45 (43%) were of low intensity; all of these were short, and less than one-third included pushing with, therefore, a recognizable element of force. The others

TABLE V.
Uca rapax. MUTUAL ACTIVITY IN ENCOUNTERS BETWEEN AGGRESSIVE WANDERERS AND BURROW HOLDERS.
(Locality and dates as in Table II, p. 56. Encounters were included in this table only if they were
observed from a manus rub beginning.)
Key: AW Aggressive wanderer
BH Burrow holder
AW/BH Activity in turn by aggressive wanderer and burrow holder

Combat Type Number	Combat Composition	Total Combats Observed	Division of Components Between Opponents				
			Components		Actors		
				BH	AW/BH	AW	Identity unknown
1	Manus rub	6	Manus rub	4	2
2	Manus rub + dactyl slide	11	Manus rub Dactyl slide Manus rub + dactyl slide	.. 4 5	.. 2 ..	4	2
3	Manus rub ± dactyl slide + heel-and-ridge ± taps	6	Manus rub Dactyl slide + heel-and-ridge Heel-and-ridge Heel-and-ridge with taps	.. 1 1 4	3	3
4	Manus rub ± dactyl slide + interlace ± taps	4	Manus rub Dactyl slide Dactyl slide + interlace with taps Interlace Interlace with taps	1 .. 1 .. 2	.. 1	1 1 ..	2
5	Manus rub + dactyl slide + heel-and-ridge with taps + interlace	1	Manus rub + dactyl slide Heel-and-ridge with taps Interlace	.. 1 ..	1 1
Total		28		24	6	10	7

TABLE VI.
Uca rapax. MUTUAL ACTIVITY IN ENCOUNTERS BETWEEN TWO BURROW HOLDERS.
(Locality and dates as in Table II, p. 56. Encounters were included in this table only if they were observed from a manus rub beginning.)

Key: Y Larger burrow holder
y Smaller burrow holder
Y/y Activity in turn by larger and smaller burrow holders
Boundary Region approximately midway between burrows of opponents

Combat Type Number	Combat Composition	Total Combats Observed	Place	Division of Components Between Opponents			
				Components		Actors	
				Y	Y/y	Y	y
1	Manus push + manus rub	2	2 at y's burrow	Manus push	1	..	1
				Manus rub	..	1	1
2	Manus rub	3	2 at Y's burrow 1 at y's burrow	Manus rub	..	3	..
			
3	Manus rub + dactyl slide	5	3 at y's burrow 2 near boundary	Manus rub	..	4	..
				Dactyl slide	1	3	..
				Manus rub and dactyl slide	1
4	Manus rub + heel-and-ridge ± taps	4	2 at Y's burrow 2 at y's burrow	Manus rub	1	2	..
				Heel-and-ridge	1
				Heel-and-ridge with taps	1	..	1
				Manus rub + heel-and-ridge with taps	1
5	Manus rub + dactyl slide + interlace with taps	1	1 near boundary	Manus rub	1
				Dactyl slide	..	1	..
				Interlace with taps	1
6	Manus rub + dactyl slide + heel-and-ridge with taps + interlace	1	1 at y's burrow	Manus rub	..	1	..
				Dactyl slide	1
				Heel-and-ridge with taps	1
				Interlace	1
Totals		16		9	16	6	6

TABLE VII.
U. rapax. DIVISIONS OF 104 COMBATS OF KNOWN DURATION.

Intensity	Duration Less Than 20 Secs.		Duration More Than 60 Secs.		Total
	With force	Fully ritualized	With force	Fully ritualized	
Low	10	35	0	0	45
High	4	46	4	5	59
Total	14	81	4	5	104

were composed of manus rubbing alone and always appeared wholly ritualized.

The remaining 59 combats (57%) each included one or more high intensity components, usually preceded by manus rubs. Eight (less than 14%) included forceful endings; about five-sixths (83%), therefore, were wholly ritualized.

As will be evident in the following sections, the figures of greatest interest are those in the duration divisions within high-intensity combat. Here 50 (85%) of the combats were of short duration, and of these 4 (8%) ended forcefully. In contrast, of the 9 (15%) long combats, 4 also ended forcefully, but the percentage (44%) was much higher.

Seven of the 9 long combats had mutual components; 3 of these 7 had forceful endings, including the eviction of a burrow holder by an aggressive wanderer. Both of the evictions in the sample came at the end of a long fight. Six of the long combats involved an aggressive wanderer, a proportion roughly in agreement with wanderers' occurrence in the combat sample. Finally, 8 (88%) of the 9 long fights were heteroclaved—a very different proportion from the 50% characteristic of the sample.

In summary, in a sample of 104 combats all but 9 lasted less than 20 seconds. Each of these 9 lasted more than a minute and contained high-intensity components. Proportionately more of these long combats occurred between right- and left-clawed crabs, more had mutual components, and more ended forcefully than did short combats.

F. Postcombat Behavior

After most encounters between *rapax* males, the opponents promptly resumed their precombat activity. Aggressive wanderers passed on through the population, instigating new combats and engaging in other activities, as already described (p. 53). Burrow holders, returning with equal completeness to all their former activities, first resumed waving.

Almost one quarter of all encounters suffi-

ciently observed, however, were followed by detectable changes in behavior. Of all observed combats, both opponents were watched long enough in 148 examples to form a suitable basis for an examination of such changes and of combat composition when subsequent changes did not occur. These alterations in behavior were of two kinds: either the aggressiveness of an aggressive wanderer was reduced or there was an appreciable delay in the resumption of waving by a burrow holder. Reduction of aggressiveness in a wanderer and delayed waving by the burrow holder never followed the same combat, nor was waving ever delayed by both opposing burrow holders.

Table VIII breaks down the 148 combats where subsequent behavior was observed into a number of potentially relevant subdivisions. The first column, headed "Result," divides the group into those with behavior unchanged, waving delayed, or aggression reduced. In the second column, "Combat Class," the opponents' phases and relative size are indicated, as in previous tables, as well as, where necessary, the instigator and the site of the combat. Under "General Combat Composition" selected characteristics are isolated; these show the relative prevalence of low- and high-intensity combats, forceful components, tapping, and mutual components. It seemed that one or more of these aspects of combat might be correlated with behavior changes or the lack of them. However, no clear-cut correlation emerges. For example, neither tapping nor mutual components preclude either a delay in resumption of waving or reduced aggression; similarly, forceful endings are not necessarily followed by subsequent behavior changes. Nevertheless, certain trends are indicated. The information given by the table, in addition to the more limited data on combat duration (pp. 63, 66; Table VII), form the bases for the remainder of this section.

Class 1. Combats not followed by a detectable change in behavior—The 112 combats in this class comprise three-fourths of all in the sample;

TABLE VIII.

Uca rapax. BEHAVIOR OF OPPONENTS. FOLLOWING 148 COMBATS.
(Locality and dates as in Table II, p. 56.)

Key: AW Aggressive wanderer larger than opponent
aw Aggressive wanderer smaller than opponent
BH Burrow holder larger than opponent
bh Burrow holder smaller than opponent
M Mutual component(s) clearly present
* Burrow holders dispossessed; waving resumption delayed more than 2 minutes

Result	Combat Class	General Combat Composition								Sub-total	Total
		Low intensity only			High intensity						
		With push	No push apparent	With forceful end		No forceful end					
				No taps	With taps	No taps	With taps				
Subsequent behavior apparently unchanged	AW & bh	1	5 (1 M)	1	3 (1 M)	10			
	aw & BH	..	15 (2 M)	5 (1 M)	..	23 (6 M)	13 (10 M)	56			
	BH & bh										
	(BH=trespasser)	4 (1 M)	7	7 (3 M)	3 (2 M)	21			
	BH & bh										
	(bh=trespasser)	1	5 (3 M)	1	..	4 (1 M)	5	16			
BH & bh (on boundary)		..	6 (2 M)	3	..	9			
Subtotals		6	38	6	..	38	24	112	112		
Resumption of waving by burrow holder delayed (less than 2 minutes except as noted)	AW & bh	..	4	..	2 (1 M) *	3	2	11			
	aw & BH	..	2	1	..	3			
	BH & bh										
	(BH=trespasser)	2	3	2	2 (1 M)	9			
	BH & bh										
	(bh=trespasser)			
BH & bh (on boundary)		1 (1 M)	2 (1 M)	3			
Subtotals		2	9	..	2	7	6	26	26		
Wanderer's aggressiveness reduced	AW & bh	2	1 (M)	..	1 (M)	4			
	aw & BH	..	4	..	2	6			
	BH & bh										
Subtotals		..	4	2	3	..	1	10	10		
Totals		8	51	8	5	45	31	148	148		

61% were of high intensity. Force was detected in about 12% of all combats in the class; therefore, 88% were fully ritualized; forceful ends occurred in about 5%. Tapping was present in more than 21% of the total, never in combats where forceful ends occurred; where only high-intensity combats were counted (since tapping normally occurs only then), the percentage with tapping was 35%. Mutual components were noted in about 30%. Short combats, lasting less than 20 seconds, formed 95% of the total in a duration sample of 86 in this class.

Class 2. Combats followed by a delay in resumption of waving—Fourteen of the 26 examples in this class were between an aggressive wanderer and a burrow holder; 9 were between two burrow holders where the larger was the instigator; and 3, with the instigator questionable, occurred near a territorial boundary between burrow holders. These 26 combats form almost 18% of all combats in the sample. Waving was usually delayed by a crab at his own burrow following combat with a larger individual, either wanderer or neighbor. When a smaller crab was the instigator at the burrow of a larger crab, no postcombat waving delay occurred. Of the 26 delays, 24 lasted less than two minutes; the longer exceptions were by dispossessed crabs and are described below. The short delays included some subsequent behavior associated with combat, such as a number of the total withdrawals.

Forceful components took place in a total of 15% of the class as follows: pushing occurred in two low-intensity fights between burrow holders; two high-intensity combats, both between a large aggressive wanderer and a smaller burrow holder, resulted in eviction of the burrow holder. Because of the theoretical interest of these two fights certain combat and postcombat details are pertinent. Both included taps; one showed mutual components; neither ended in a physical upset; the duration of each was more than one minute. After the first dispossession, the wanderer descended the burrow, then emerged and began waving. Meanwhile, the former occupant assumed the low posture and moved off giving no response to the threats of neighbors. Eventually he retired down an empty burrow some six feet away, where he plugged the mouth and remained at least until the next low tide. In the second example the wanderer descended the burrow after the occupant left, emerged within a few seconds, and then abandoned it to continue his precombat behavior as a continuing aggressive wanderer. Meanwhile, the evicted burrow holder had been circling around in the low posture; as soon as the wan-

derer left, this crab resumed possession, descending briefly, emerging and waving promptly. The entire delay, in addition to the combat's 1.5 minutes, lasted 2.4 minutes, in contrast to the indefinite delay in waving following the first eviction.

Throughout Class 2 tapping was absent in all fights with forceful ends except in the two just described, which ended in eviction. Tapping was present in 25% of the remainder, or almost 50% of those of high intensity without force. Mutual components were absent in low-intensity combats but present in 27% of those of high intensity, including one of the evictions, and in 15% of the entire class. Short combats formed 67% of the total in a duration sample of 15.

Class 3. Combats followed by a reduction in the aggressiveness of a wanderer—Of the 90 combats between an aggressive wanderer and a burrow holder, 10 (11%) were followed by reduced aggressiveness. These 10 combats were distinguished as follows: In 40% the wanderer was the smaller crab; 60% were of high intensity and included all combats in which force was detected; these forceful endings occurred in 83% of high-intensity combats or 50% of the total in the class. Taps were included in 40% of the total, most of them in combats with forceful ends. Mutual elements appeared in 20% of the combats, all high-intensity, with and without forceful ends. Short combats formed 83% of the total in a duration sample of 6.

Comparison of combat characteristics in relation to subsequent activities—When the above classes of combat are compared, five points emerge that seem noteworthy in spite of the small samples. First, in combats followed by the reduced aggressiveness of a wanderer, forceful endings were more numerous than in combats either not followed by behavior changes or with a subsequent delay in resumption of waving. Second, long combats were most numerous in the class followed by delayed waving, less so among those resulting in reduced aggression, and rare among encounters with no detectable results. Third, mutual components were relatively fewer in combats followed by changes in behavior. Fourth, tapping was usually absent from encounters with forceful endings; this absence is probably correlated with the frequently prompt cessation of combat after tapping. When tapping did occur in the course of a fight ending forcefully, subsequent behavior was changed. Finally, after combat any changes in behavior were usually shown by the smaller crab.

Summation—because this study was made entirely in the field among unmarked crabs, few

hints of summation were observed. I have in fact obtained reliable notes on the subject in only seven pairs of combats. Two of these involved examples where the actor's behavior changed following the second encounter; in each the encounter was less intensive than the first and the change consisted in reduced aggressiveness of a wanderer.

When marked crabs are adequately observed, it seems certain they will show that summation plays a part in the effects of combat.

V. COMBAT IN SPECIES OF
Uca OTHER THAN *U. rapax*

Combat has now been filmed in fifteen species of *Uca* in addition to *U. rapax*. These species are scattered widely throughout the genus. The results are predictably inadequate, because no special effort has yet been made to record the various patterns in species other than *rapax*. As

stated earlier it is only recently that the complex nature of fighting and its morphological specializations have become apparent. Hence, the lack of a filmed record of any particular component by no means precludes its existence.

Data on combat in Indo-Pacific and eastern Pacific species recorded only in field notes have been omitted from this paper. The observations were made before the importance of ritualized fighting was realized and at a period when my attention was concentrated on display. During those years all combats appeared too similar to deserve full attention, in an essentially comparative study of species, since time in the field was always limited.

Several statements can, however, now be made with relative assurance in comparing combat in other species with that in *rapax*. First, the Indo-Pacific species listed in Table IX, with the exception of three species in the old, informally

TABLE IX.

BASIC COMPONENTS OF COMBAT IN *Uca* SO FAR RECORDED ON MOTION PICTURE FILM.

(Note: Minor elements are omitted because of insufficient data. Species are arranged in systematic order, in accordance with a revision in preparation; the closest relations of *U. lactea* are American species, as indicated.)

Region	Species (<i>Uca</i>)	Manus Push	Manus Rub	Dactyl Slide	Heel- and- Hollow	Heel- and- Ridge	Tapping	Inter- lace
Indo-Pacific								
	<i>dussumieri</i> (Milne-Edwards)	x	x	x
	<i>coarctata</i> (Milne-Edwards)	x	x
	<i>urvillei</i> (Milne-Edwards)	..	x	x	x	..	Dactyl only	..
	<i>bellator</i> (Petiver)	x
	<i>tetragonon</i> (Herbst)	x	..	No	..
	<i>vocans</i> (Linnaeus)	x	x	..	x	..	No	..
	<i>chlorophthalmus</i> (Milne-Edwards)	x	Dactyl only	..
	<i>inversa</i> (Hoffman)	..	x	Dactyl only	..
W. Africa								
	<i>tangeri</i> (Eydoux)	x	x	x
America								
	<i>maracoani</i> (Latreille)	x	x
	<i>insignis</i> (Milne-Edwards)	x
	<i>rapax</i> (Smith)	x	x	x	..	x	Dactyl & pollex	x
	<i>cumulanta</i> Crane	x	x	x	..	x	Dactyl & pollex	x
	<i>inaequalis</i> Rathbun	..	x
Indo-Pacific								
	<i>lactea</i> (deHaan)	x	x	x	x	..	Dactyl & pollex	..
America								
	<i>deichmanni</i> Rathbun	x	..	x

named "broad-fronted group," show more tendency to forceful fighting with less ritualization. The three exceptions are *chlorophthalmus*, *inversa*, and *lactea*.

Second, the highly ritualized heel-and-ridges of the New World crabs are represented in some Indo-Pacific species by a lifting and gripping motion differing from that in *rapax* as follows: The pollex with its large distal or subdistal teeth either grip in or do not usually pass beyond appropriate hollows near the base of the pollex. This position is in contrast to the rubbing and tapping against the oblique ridge characteristic of *rapax*, *cumulanta*, *chlorophthalmus*, and *inversa*. The dactyl, however, holds in all a position similar to that in *rapax*, against the outer part of the manus. Only in broad-fronted *lactea* has the pollex been seen to make a series of taps in the hollow at the inner base of the pollex.

Several species typically shift from low to high intensity in a manner different from that of *rapax*. In *tangeri*, *maracoani*, *insignis*, and *inaequalis* the chela tips are turned downward, the mano-carpal joint raised, and the chelae engaged in this position, after which they swing once more to the horizontal. In all the other species in which high-intensity encounters were filmed, the chelae engaged in the horizontal position, usually at the end of a manus rub.

The variation in dactyl slides is great, as in *rapax*. Whereas the detailed study of *rapax* makes it possible to state the normal position of the dactyl during a slide, in other species the paucity of material and lack of information on individual social situations make any further statements unproductive.

VI. DISCUSSION

Two challenging aspects of fiddler combat are the obscurity of its functions and the complexity of its ritualizations. As long as the functions of fighting remain uninvestigated its ritualizations can be only superficially understood. Because of the new data presented, however, it seems timely to comment on possible functions for combat and to suggest reasons for its ritualization. The section continues with preliminary remarks on the possible origins of the components and on comparisons with combat in other animals. It closes with suggestions for further research.

A. Functions of Combat in *Uca*

A general discussion of territoriality in fiddler crabs lies beyond the scope of this paper. Here the subject will be mentioned only to the extent necessary to give a frame of reference for the consideration of combat.

In this genus the territoriality of breeding

males appears to be not at all concerned with the optimum distribution of the population in respect to the food supply. Only males in the display (waving) phase, during which mating takes place, behave aggressively toward individuals in the vicinity of their occupied burrows, and then only toward males in the aggressive wandering phase or toward trespassing neighbor males. Aggressive wanderers, in contrast, neither wave, mate, nor remain near a particular burrow. The territories of the displaying crabs are not scattered equally through the population, nor are they usually to be found in food-rich locations.

Burrows of displaying crabs are often, instead, concentrated in slightly higher, drier parts of the intertidal zone, where food is less abundant. Here males in other phases are few or absent. Moreover, crabs in the display phase feed little in comparison with others, and when they do so, they often move temporarily to the richer, lower levels. Females in breeding condition in some species occupy burrows close to those of waving males; in others, receptive females move actively through the displaying portion of the population; after mating, while the eggs are developing, females usually inhabit burrows closer to the low-tide levels than those of any section of the population except the very young.

It appears rather that territoriality in *Uca* is concerned directly and indirectly with reproduction. An advantage of territories on higher ground may be that the displaying crabs are there more conspicuous. This could obviously be of importance not only in attracting receptive females but in the mutual visual stimulation of waving males. Again, the drier substrate may transmit more effectively the vibration signals of courtship. Finally, and probably importantly, territories on higher ground are uncovered by the tide for longer periods daily, thus giving more time for courtship; at least in the tropics receptive females are never abundant in any population of waving males and courting time is short at best. It must be emphasized, however, that displaying males in a given species by no means always gather into a lek-like formation; very often they are scattered, although in clear sight of one another, throughout the greater part of a population. The relative breeding success of individual males with burrows in different locations remains wholly to be investigated.

Possible explanations of fighting remain far from clear. It is unsurprising that each crab coming into territorial and display phases acquires a burrow in a spot appropriate for display and mating. But, for two reasons, there appears to be no need to obtain such a burrow through

combat. First, all fiddlers of both sexes and of all ages except the very young can dig new burrows quickly and efficiently. Yet they do so only in emergencies brought on by predators or by an intruding tide. In contrast, when a large crab evicts a small one, he enlarges the burrow suitably, with neither hesitation nor hurry. Furthermore, few areas are so crowded that there does not appear to be ample space, empty and undefended, among displaying males where new burrows could be dug.

Second, and probably more important, in all displaying populations that I have adequately observed, empty burrows are plentiful among those of displaying individuals. They have been abandoned by crabs not at the time in a burrow-holding phase; as the tide recedes, these crabs simply dig their way to the surface and go elsewhere. Yet an aggressive wanderer, unless his aggressiveness has been reduced by a fight with a burrow holder, either pays no attention to these empty burrows, or pokes into them with cheliped or ambulatories, briefly and superficially; then he moves on. These empty burrows always appear to be considerably more numerous than are the wanderers, so that no difficulty in encountering such a hole seems to be involved.

Although occasionally an aggressive wanderer stops slightly longer at a burrow occupied by a nondisplaying crab, any attempt to dig out such a crab is rare and little effort is expended. I have never knowingly seen a combat between a crab that is not in display phase and a wanderer, or between two wanderers.

In fiddler crabs no harems are maintained and single females seem never to be direct causes of intermale combat. Occasionally a male even abandons an advanced courtship, attracted by a combat between two other males.

The immediate goal of an instigator does not in fact seem to be the taking over of a suitable burrow as a center for display or a direct competition for females. Rather, the apparent aim is a combat with a displaying male.

The combat itself, as has been described in detail for *rapax*, is usually fully ritualized, with no apparent component of force; in most cases it results in no detectable change in the subsequent behavior of either crab. One or the other withdraws his claw from contact with that of his opponent; the aggressive wanderer resumes his progress through the population, threatening and entering into new combats; the burrow holder promptly resumes display, its intensity undiminished. In one such *rapax* combat in nine, however, a wanderer's aggressiveness was reduced; in one in 45, the burrow holder was dispossessed and the wanderer took over. Less

intensive observation of other advanced species have yielded corroborative observations: The wanderer's behavior is similar and only rarely is there a detectable result. In those instances where a wanderer actually takes over a burrow he sometimes assumes the display phase at once; more often, he does not wave, but shortly abandons the burrow and moves on, his aggressiveness maintained and his territorial drive still in abeyance.

With these figures in mind it seems likely that combat may sometimes either advance or retard the assumption of territorial and waving phases by the wanderer. Summation, as suggested on p. 68, may well play a part here that the field techniques in use could only suggest. Combat, then, may serve as a mechanism for ensuring that suitable burrows for display are not taken over by males in subbreeding condition; nevertheless, the availability of empty burrows, noted above, forms an obvious argument against this view.

The function of combat will now be examined from the point-of-view of the burrow holder. If this displaying crab is not vigorous enough or sufficiently motivated to fend off an aggressive wanderer, he may be in an inadequate condition for breeding and should not, from the point of view of selection, be left in a position to attract receptive females. Yet many vigorous burrow holders, in other species as in *rapax*, withdraw partly or wholly from an incipient combat, even in the frequent instances where the approaching wanderer is the smaller crab; then the burrow holders resume waving and courting promptly and strongly when the wanderer has departed. The role of this withdrawal behavior in the pattern of combat remains puzzling.

After combat, however, one *rapax* in six delays waving, while one in 45 loses his burrow, with a consequent postponement of resumed display. These relative numbers agree well with impressions received in numerous more casual observations of combat in other species.

In examining the possible selective values of fighting and its ritualization a distinction should be kept in mind between these two visible results—namely reduced aggressiveness and delayed waving. Since all burrow holders are in the display phase and, as part of that phase, in a threatening and fighting mood toward both aggressive wanderers and trespassing neighbors, it seems that a postcombat reduction in aggressiveness by a wanderer normally would result only if he were not ready for territorial-display-mating behavior. In that case the "loss" of a combat would be a selective advantage. On the other hand, a reduction of display time for a burrow holder

through prolonged combat would be a disadvantage.

A reasonable suggestion, therefore, appears to be that the ultimate value of combat, regardless of the role of ritualization, lies in preventing suboptimal males from wasting the breeding time of the population by attracting receptive females. This explanation does not, however, account for all the facts. It takes no account of combats, almost all fully ritualized and resulting very rarely in waving delays, between vigorous burrow holders. Again, the function of down-pushes remains unexplained. Here one burrow holder, far from endeavoring to take over the burrow of his neighbor or at least to dig the occupant out and engage him in combat, simply thrusts him forcefully underground before returning to his own burrow and resuming display.

When viewed as a whole it seems that the function of combat may lie primarily in stimulating and synchronizing mating behavior. As in so many other groups of animals where such an effect is suspected, proof awaits work in endocrinology and neurophysiology.

Similarly in need of the attention of physiologists are two strong impressions that recur during fieldwork on *Uca*. One is that combat may serve to release tension in the actively courting section of the population. The other impression, particularly compelling when one is watching ritualized mutual encounters, is that combat appears often to be in progress for its own sake. The attention of a third crab is sometimes drawn to a nearby combat; he may then either interrupt or engage one of the participants after the end of the first encounter. Even more suggestive are the sequences of high ritualization discussed below.

B. The Question of Adaptive Values of Combat Ritualization

As shown in previous sections, a large majority of combats in *Uca rapax* show no detectable element of force and hence may be termed fully ritualized. More casual observations on other species indicate that ritualization is similarly prevalent throughout the genus. In searching for the selective advantages of ritualization the immediate effects of individual combats have proved unilluminating. As is well known, even the most violent fights in *Uca* practically never result in physical damage; no injury at all was ever seen in *rapax*. It seems, therefore, that a protective function, which has been considered obvious in the ritualized encounters of many well-armed animals, is not now of importance in fiddler crabs.

Again, the data in this paper on *rapax* give

no evidence that ritualized encounters are any more likely than the uncommon forceful fights either to promote or to prevent behavior changes in an opponent. This is true in general both of reductions in the aggressiveness of a wanderer and of delays in resumption of waving by a burrow holder.

The only apparent advantage of ritualization in *rapax* seems, rather, to lie in the shortening of combats. The counts so far made indicate clearly that ritualized encounters are not only far more numerous than those including components of force but also that they are shorter, most lasting less than 10 seconds. In contrast, forceful fights continuing more than one minute are usual. This is true whether or not a forceful combat results in subsequent visible behavior changes for either crab. While this difference in duration appears to have no obvious importance for an aggressive wanderer, the shortening of combats through ritualization may well be a selective advantage through its effects on burrow holders.

This suggestion is based on both the ecology and the mating behavior of *Uca*. Since they court only during low tide, and are usually further restricted by other requirements, both meteorological and physiological, their periods for courtship and mating are limited. Combat and courtship cannot proceed simultaneously and, in *Uca*, the combats of males seem to hold no attraction whatever for females. Therefore it seems clear that, by shortening combats, ritualization ensures that courtship opportunities are minimally reduced.

It may be that an important factor in waving display lies in its stimulating effect on other males, or in the synchronizing of breeding activities. Here, too, a shortening of each combat would advantageously shorten the time during which one or two wavers did not contribute to the communal effect.

One characteristic of ritualized combat becomes increasingly apparent with continued observation. This consists in the leisurely, formalized, and wholly unforceful cooperation sometimes apparent between the two opponents. A highly ritualized encounter in *rapax* may run about as follows. An instigator, whether wanderer or neighbor, approaches a burrow holder. A rub by one or both crabs, outer manus against outer manus, usually follows. Next, the instigator sometimes holds perfectly still while his opponent slowly eases his chela into the actor's slide position; the two crabs may then reverse the role, the shift being accomplished slowly, without fumbling, and with the apparent cooperation of the crabs. In a few moments they may

progress to a similar alternation of heel-and-ridging or, in heteroclawed encounters, to an alternation of heel-and-ridging with interlaces. In other examples a single opponent may be the actor throughout, the second crab holding himself quietly. When the actor breaks off, both crabs move apart and resume their pre-encounter activities.

Observation of these encounters gives a strong impression that they provide one or both crabs with satisfactions that are not concerned in direct goals, such as taking over a burrow or evicting a trespasser; the activity itself seems to serve as the goal. We know nothing at all yet about the means of conferring satisfaction—whether through the performance of the motions, or through the reception of associated sensory stimuli.

If ritualization does indeed operate selectively through shortening combats and thus providing more time for courtship, then an obvious pressure would be toward even shorter ritualized encounters. Ultimately the action might be reduced to a token touch of mani or single rubs of ridges by briefly overlapping chelae.

This trend is not apparent. According to our present knowledge, the socially advanced species have the largest repertoire of combat actions and the most extensive structural specializations for high-intensity encounters. If ritualization shortens combats, then further elaboration could nullify the effect. Occasional prolonged encounters in *rapax*, fully ritualized and elaborately mutual, suggest that this process may prove to be a factor in current evolution.

C. Derivation of Components

Too little comparative work has yet been done to discuss the comparative ethology of combat in *Uca*. Nevertheless it seems worthwhile to suggest two basic derivations that may be kept usefully in mind during future studies.

It seems likely that high- and low-intensity components have been derived from different sources. These are, respectively, from forceful fighting itself and from the fronto-lateral threat gesture common to most crabs. If the direction of evolution has been, as seems apparent, the reduction of forceful combat through ritualization, one logical point for the application of a deterrent would be immediately before the grip. The high-intensity components all appear to have originated directly from unritualized forceful grips. All take place with the two claws partly or wholly in a position for grasping each other; when, rarely, a ritualized encounter proceeds to a grip, little or no change in basic claw position is made. Unsurprisingly, specializations

appear to have been added one in front of another, the interlace of *rapax* being perhaps the closest now known to the original fighting grip. The ultimate ritualization, then, would be logically the low-intensity manus rub.

However, the manus rub seems most credibly to have evolved from the warding-off lateral threat gesture, which is almost universally present in crabs. But threat gestures in many animals are themselves certainly to be understood as ritualizations of fighting, where a weapon, impressive size, or other potential advantage is exhibited, usually with exaggeration or embellishment. By these criteria, the threat gestures of crabs, including *Uca*, qualify as ritualized fighting. It seems that in *Uca*, however, manus rubbing is a further ritualization derived from a basic threat posture.

D. Comparisons with Ritualized Combat in Other Animals

The ritualizations of combat through threat displays are of course endlessly varied among animals, perhaps culminating in the displays of sound, color, and movement in many territorial birds. In fiddler crabs parallels are close.

In encounters where two individuals come actually into contact, however, comparisons are far less satisfactory. Checked point by point with *Uca* combat, the harmless poking and heaving of fighting beetles or the ritual butting and kicking of ungulates are simple, coarse, and slow while the associated structures seem relatively unspecialized. A search of the literature has not yet yielded, even among deer, an apt comparison. It seems that no buck rubs a certain antler prong gently against a different prong, suitably shaped, on his opponent's armature, then holds still while the other gets into position and rubs in turn and, finally, passes on to a further step in the sequence. Schaller's (1967) detailed comparative study of combat in eight Indian ungulates indicates no such refinements. There seems to be in fact not even a rough analogy to perhaps the highest *Uca* specialization of all, where adaptations exist even to the different requirements of opponents with the ritualized weapon on the same or opposite sides of their bodies. In other decapod crustaceans it seems certain that many spines and ridges, that have been as in *Uca* of purely taxonomic interest, will prove to be as functional as in fiddlers, and perhaps in similar fashion.

E. Areas for Further Research

The following aspects of *Uca* combat particularly need attention before the wider implications of the subject can be investigated.

1. *Sensory aspects*—It is not yet known whether the rubs and taps of combat are perceived by the crabs and, if so, which senses are involved. Acoustic elements will probably prove to be part of the pattern of fiddler combat as in their other types of social behavior; I have heard rasps and clicks during examples of each of the components. It seems likely, however, that tactile sensations are also important. For that reason the term "stridulation" has not been used in this contribution.

2. *Neurophysiological and hormonal aspects of phase and of behavioral changes following combat*—These basic problems are more than ready for investigation. They should be undertaken in a laboratory adjacent to wild populations, or at least in one equipped with a large crabber. This specialized terrarium should include provisions for artificial tides; for controlled salinity, temperature, and light; for a substrate natural for the species, changed at suitable intervals; and for frequent restocking. In short, adequate results could not be obtained from fiddlers in finger bowls.

3. *Duration of individual combats*—The data in the present paper on the timing of combats are particularly inadequate in view of the tentative conclusion that the primary function of ritualization in *rapax* is the shortening of combat. In future work on all species, the behavior associated with combat should certainly also be timed.

4. *Combat at night and underground*—The occurrence and form of encounters at night and in burrows need examination. The deep pits at the pollex base that in some Indo-Pacific forms apparently serve as "brakes," and are often marked by puncture wounds, are represented in *rapax* and its relations respectively by slight depressions and faint scratches. No gripping has ever been seen in *rapax* in this position; perhaps such a grip is used only when an intruder enters an occupied burrow. Observation burrows can be devised in the laboratory.

5. *Mathematical analysis*—The distinctness of components in most combats at first glance makes a mathematical approach to combat analysis seem feasible and attractive. But success in such undertakings is endangered by a number of pitfalls. Quantitative analysis could be misleading unless based on accurate, detailed knowledge of the full combat repertory and its related behavior in the selected species, and on influences of seasonal and other rhythms. The principal threats to the significance of conclusions include: the difficulty of observing the exact beginnings of combats; the partial distinctions between homoclaved and heteroclaved encoun-

ters; the existence of mutuality and the difficulties in distinguishing it; the hard-to-gauge degree of basic aggressiveness in contrast to the cooperation sometimes apparent; the need for definite establishment of the phases of the opponents; the frequent irregularities in combats involving aggressive wanderers; and the difficulty of assessing the effects of summation.

6. *Marked crabs in a fenced wild population*—Many of the difficulties listed could be reduced by fencing a suitable intertidal area, large enough to give wanderers space to move about normally.

7. *Comparative ethology*—Contrary to my earlier conclusions, it is now clear that interspecific distinctions in combat behavior are numerous enough to make their comparative study highly rewarding. While the differences are not nearly as striking as in display there is no question but that they both illumine evolutionary trends in species groups and show most interesting steps in the development of combat ritualization.

8. *Instigation and frequency of combat*—The conditions leading to combat between individuals and controlling its frequency in a population deserve the closest attention. Most of the following factors, all virtually uninvestigated, will probably prove pertinent: precombat threat behavior, length of time since phase of each opponent began, age, individual variation, semilunar and other rhythms, population density, and infra-specific differences.

VII. SUMMARY

This contribution concerns a field study of combat between male fiddler crabs. Except for preliminary comparisons with a few other species, the report is based on several hundred combats observed in a population of *Uca rapax* (Smith) in Trinidad. Descriptions of the various aspects of the subject were derived from between 104 and 180 examples watched or photographed in sufficient detail for each purpose.

The combat pattern in *rapax* shows seven distinct components, five of them highly ritualized and each of the five associated with particular morphological specializations. The frequency of three of the components is related to the juxtaposition of the large claws: when one crab has the claw of the right side enlarged and his opponent that of the left, the components tend to be different from those observed when both crabs have the large claw on the same side. Most combats last only a few seconds and infrequently include the unritualized components of force; when they do so, the fights are often longer and may last several minutes. Two or more ritualized elements, usually performed in a fixed sequence,

compose most encounters. In each component one crab rubs and sometimes taps with teeth on his own claw a tuberculated ridge or other particular structure on the claw of his opponent. Many combats are mutual in the sense that each crab performs at least one of the components; sometimes the same component is performed by each crab in turn. The sensory aspects of ritualized combat have not yet been investigated.

Combats divide sharply into two categories. The first takes place between an aggressive wanderer and a burrow holder in the display phase; its components are often irregular; practically all combats ending in forceful grips and upsets belong in this category. In the second, the opponents are two neighboring burrow holders; irregularities and force are both uncommon. The relative size of the opponents is a factor in the development of combats and in various associated activities.

The great majority of combats, whether wholly ritualized or not, result in no detectable change in the behavior of either crab. Each opponent continues either to wander aggressively or to wave beside his own burrow. Only twice, both after long fights, was a burrow holder dispossessed by an aggressive wanderer with an associated indefinite delay in further waving and, therefore, courting activity. One combat in nine results in a reduction of aggressiveness by the wanderer; one in six is followed by a very short delay in waving resumption by a burrow holder. Combat does not appear to be concerned, even indirectly, with the food supply; it neither involves nor attracts females; it appears to be unnecessary for the securing of suitable burrows as display centers and mating sites.

It is suggested, therefore, that the functions of combat must be sought in indirect physiological needs connected with reproduction, such as stimulation or the release of tension. It is further suggested that the principal selective advantage of ritualization lies not in the prevention of physical injury or of loss of display phase but rather in the shortening of combats. In this way less of the brief time suitable for courtship is lost in fighting.

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EXPLANATION OF THE PLATE

PLATE I

Combat in *Uca rapax* (from 16-mm. motion picture film). See text, pp. 57-59.

FIG. 1. Tap following a heel-and-ridge in homo-clawed combat. The actor is the crab on the right. His dactyl is striking the heel of his opponent's manus while his pollex is free.

FIG. 2. Same combat as in Fig. 1. Alternate stroke

showing the actor's pollex against his opponent's invisible oblique ridge, on inner side of manus.

FIG. 3. Interlace in a heteroclaved combat. The actor is on the right. The teeth near his dactyl's base are starting to rub downward against the ridges of his opponent's inner manus, which parallel the dactyl's base.

FIG. 4. Same, near end of downward stroke of rub.



FIG. 1



FIG. 3



FIG. 2



FIG. 4

COMBAT AND ITS RITUALIZATION IN FIDDLER CRABS (OCYPODIDAE)
WITH SPECIAL REFERENCE TO *UCA RAPAX* (SMITH)

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Published April 15, 1968

Influence of Climate on the Distribution of Walruses, *Odobenus rosmarus* (Linnaeus). I. Evidence from Thermoregulatory Behavior.

FRANCIS H. FAY¹ AND CARLETON RAY²

(Plates I-IV; Text-figures 1-2)

INTRODUCTION

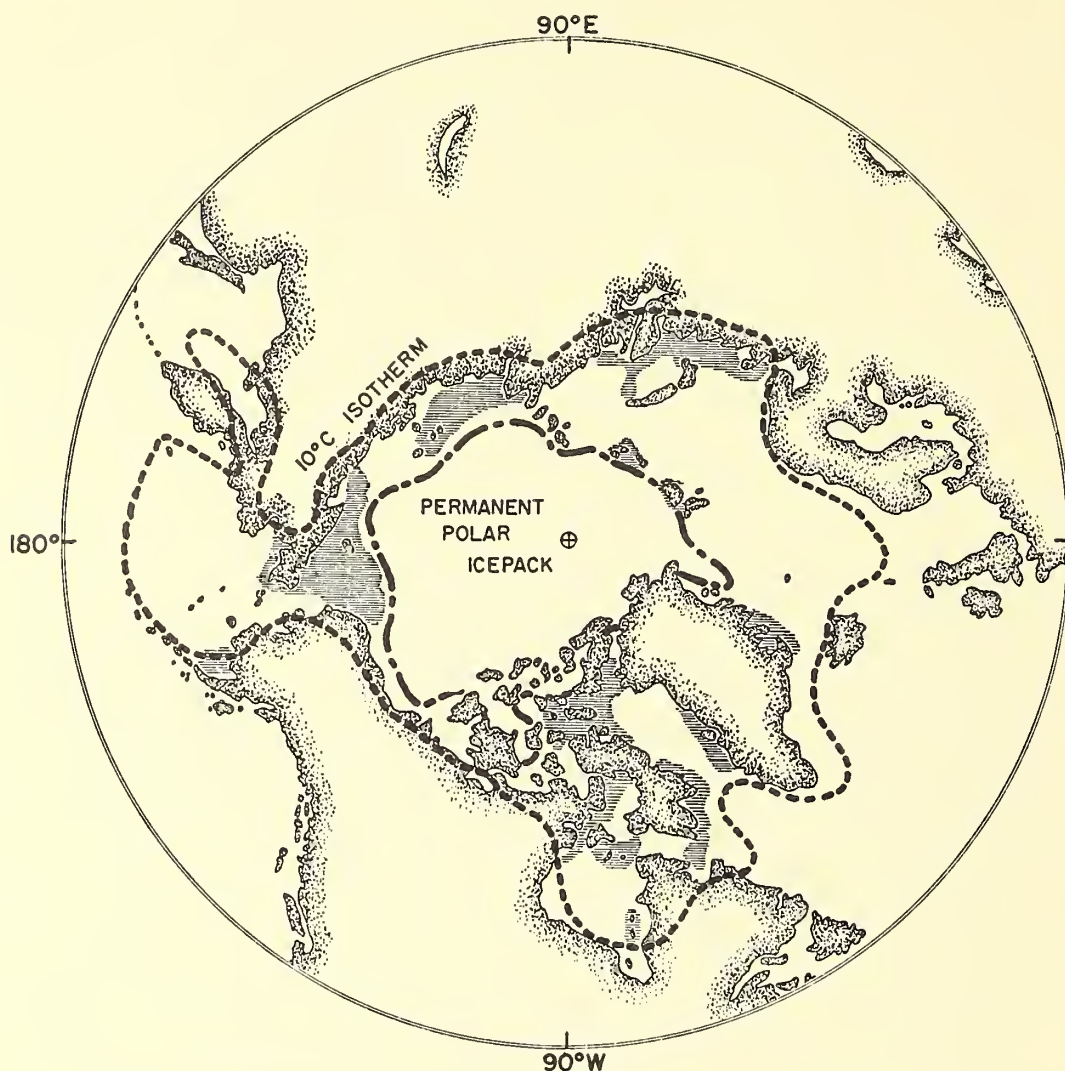
THE walrus is one of a group of pinnipeds typically associated with the ice front in northern seas, but like most of the others, it is by no means restricted to the front. Some walruses occur as much as 1,000 miles south of it in summer and some as much as 500 miles north of it in winter. Within this range, the walrus resides chiefly in the shallow waters of the continental shelf, where its food of mollusks and other benthic invertebrates is obtained at depths of 80 meters or less (Vibe, 1950). The area occupied by these mammals on a year-round basis thus comprises parts of two marine zoogeographic zones, the Arctic and the Boreal or subarctic (Ekman, 1953; Zenkevitch, 1963), but does not include the full extent of shallows in either one. The failure of walruses to occupy all of the shoals and inshore waters of the Arctic Zone seems to be clearly a matter of their inability to penetrate regularly into the polar ice-pack or to obtain food in some areas where mollusks are scarce (Fay, 1957). Their occupation of only the northern part of the Boreal Zone may be due to restrictions imposed by the climate, which varies from subarctic in the

northern part to low temperate in the south. A correlation between the southern limit of the walrus' range and isothermal lines was noted more than a century ago by von Baer (1838, *vide* Allen, 1880:91), and we find this to be generally true today. The majority of these animals occurs in areas where monthly mean air temperatures are from -15 to $+5^{\circ}\text{C}$, and only a few vagrants range south of the 10°C isotherm at any time (Text-fig. 1). In the study reported here, we set out to test the theory of a southern climatic boundary, not by comparing distribution with thermal conditions, but by examining the behavioral and physiological responses of walruses to subarctic and temperate climates. In this paper we report on the behavioral aspects of the study; the physiological findings are reported separately (Ray & Fay, 1968).

The material presented here is of two kinds. First are descriptions of the postures and other physical adjustments of walruses that affect the amount of exposed surface area and could influence the rate of heat loss from the body to the ambient. Second is a quantitative comparison of the weather when the animals were *out* versus *in* the water. Walruses spend about as much time out of the water as in it, and the frequency and duration of their lying out seem to be affected by the weather conditions at the time (Shulldham, 1775, *vide* Allen, 1880:67; Hayes, 1867:404; Nikulin, 1947). Since their presence in or out of the water may depend also on the normal alternation of activity and rest, we have included an investigation of the normal activity rhythm.

¹Biologist, Arctic Health Research Laboratory, Public Health Service, U.S. Department of Health, Education, and Welfare, College, Alaska.

²Department of Pathobiology, School of Hygiene and Public Health, The Johns Hopkins University, Baltimore, Maryland. Formerly, Curator, New York Aquarium, New York Zoological Society, Coney Island, New York.



TEXT-FIG. 1. The north polar region, showing the present distribution of walrus in summer in relation to the minimum extent of the permanent ice pack and the isotherm of 10°C mean air temperature for July.

MATERIALS AND METHODS

Information on the behavior of free-living walrus was obtained mostly by Fay during the period 1952 to 1965, in the vicinity of St. Lawrence Island, Alaska, just south of Bering Strait. In the course of approximately 400 hours spent hunting walrus with the Eskimos of that area, at least 1,190 adults, subadults, and juveniles were seen, plus many calves not included in the counts. More than 8,000 others were seen during aerial surveys of the Bering Sea. Most of

these animals were sighted during the daytime, between 0800 and 1600 hours, when more than four-fifths of them were lying out on ice floes; the rest were swimming or feeding in the water. Although the Eskimos' objective during the hunts was to kill the animals for food, observation of undisturbed animals was usually possible for several minutes before the shooting occurred. In that time, behavior of potential thermoregulatory value was observed.

Most of the field observations were made in May, when the Pacific walrus population was

concentrated in the northern end of the Bering Sea. The behavior of the animals in that time and place is assumed to have been representative of their responses to weather slightly warmer than the mean for their year-round environment. Observations in the vicinity of St. Lawrence Island during January to March provided some indications of the reactions to the coldest weather to which walruses are ordinarily exposed in the Bering Sea region; the island is the northern limit of their range at that time (see Brooks, 1954). For observation during the warmest weather in summer, Fay went to Round Island ($58^{\circ} 30' N$, $160^{\circ} W$), Bristol Bay, Alaska, the southernmost area regularly occupied by Pacific walruses in that season. About 1,500 males were observed there during a four-day visit at the end of June, 1958.

The data obtained in the field on the activity rhythm and reactions to weather were mostly notations of the time, location, and number of animals seen *in* (swimming) or *out* (resting) of the water. Only those animals that were undisturbed were counted; alarmed walruses invariably took refuge in the water. These notes were later correlated with meteorological data recorded by us or by personnel of a nearby weather station. The data were biased to the extent that it was usually not possible to observe the animals during periods of extremely stormy weather.

Our information on the behavior of walruses in captivity was obtained from 1957 to 1963, principally by Ray at the New York Aquarium. The animals from which most of the information was obtained were an adolescent male, probably of Greenlandic origin, and a juvenile female from the Bering Sea. Both had been in captivity since infancy. Data on their activity rhythm and reactions to weather were obtained in 1960, during a six-month period of close surveillance. At that time, the male was about five years old, and the female was about one year old. At regular intervals each day, notations were made whether each animal was in the water or hauled out on its resting platform, and these were correlated with hourly weather recorded by the U. S. Weather Bureau, 17 Battery Place, New York City. The weather records were less applicable than on-site micrometeorological data would have been, but the conditions described by them were similar to the general weather at the aquarium. One notable exception to this was wind velocity; winds were stronger and more frequent at the Battery than at the aquarium, and within the sheltering walls

of their enclosures the animals were further removed from the effects of all but strong winds.

From January 18 to May 30, notations on activity were made several times daily between 0800 and 1600 hours and, after May 30, also at 0200, 0600, and 2200 hours. At 0800 hours daily, throughout the six-month period, a notation was made also of the presence or absence of feces on each animal's resting platform. Since the animals seldom defecated on the platforms except when they stayed out for an hour or more beforehand, we used this as an index of their having spent some time out of water during the night. In June and July, when both this index and their regular nighttime observations were recorded, they showed close agreement.

The captives were kept in separate, walled enclosures about 20 meters apart and were visually, but not acoustically or olfactorily, isolated from each other. Since vocal communication between them was rarely detected, and since neither animal was sexually mature, we are confident that any intercommunication that did occur did not seriously influence their behavior. The male's enclosure also held three gray seals, *Halichoerus grypus*, but the walrus was dominant over these and virtually unaffected by their presence. Neither did the presence of human spectators seem to distract either animal to the extent that its activity rhythm was affected. Although the spectators were not ignored while the walruses were swimming, the animals were largely oblivious to all human activity when they hauled out to rest. The aquarium was open to the public from 1000 to 1700 hours daily to May 30 and from 1000 to 2200 hours thereafter. The only significant human influences on the behavior of the animals during that time were the daily feedings; each animal usually hauled out on its resting platform when the keeper arrived with the food at 1030 to 1100 hours and 1530 to 1600 hours. Spot observations were recorded at those times each day before feeding.

The juvenile female was one of 21 individuals obtained at St. Lawrence Island between 1958 and 1963. All of these were very young animals when captured, ranging in age from newborn to three or four weeks old. They were held in pens on the island for up to two weeks before being transferred by aircraft to the aquarium. In that time, we obtained information on their reactions to the local weather and, in a few cases, to a wide range of experimentally imposed thermal conditions. Comparative information on their reactions to hot summer weather was obtained after their arrival in New York.

RESULTS

Regulation of Surface Exposure in Air

Four methods were used by walruses to regulate exposure of their body surface and appendages to the ambient while at rest out of water. These were huddling, posture, fanning, and selection of substrates. These will be considered separately, though they often occurred simultaneously.

Huddling. Of nearly 10,000 walruses seen by us from small boats and aircraft, less than three per cent were alone; the rest were in groups of from two to several hundred. The mean size of the groups tended to be smallest when the animals were in the water, larger when they were on ice, and largest when they were on land (Table I). One characteristic of each group resting on

TABLE I.
GROUP SIZE OF WILD PACIFIC WALRUSES
IN RELATION TO THEIR LOCATION.^a

Location	No. of Animals	No. of Groups	No. of Animals per Group	
			Range	Mean
In water	339	94	1- 50	3
On ice	6274	388	1-600	16
On land	3254	21	1-850	155

^a From unpublished data obtained by J. W. Brooks, K. W. Kenyon, A. Thayer, and F. H. Fay during aerial surveys and observation from small boats, Bering Sea, 1952 to 1962.

ice or land was the intense mutual contact between its members, which lay "... huddling like swine, one over the other" (Cook, 1822:680). This is at once apparent to anyone seeing a resting herd for the first time (Plate I), and it has been mentioned many times previously in accounts by naturalists and other explorers of arctic regions (e.g., see review by Allen, 1880: 107-121, 178-180). In captivity, also, walruses show a high degree of gregariousness and thigmotaxis; when two or more of those that we studied were kept in the same pen, they almost invariably slept huddled together. We estimated that the usual extent of contact in groups, both in the field and in the aquarium, was about 20 per cent of the total body surface per animal.

The degree of mutual contact within groups did not appear to vary seasonally, with latitude or with air temperature or other weather conditions. Herds on the beach at Round Island in June, under clear skies and in 14°C air, were apparently as tightly packed as those on the ice

in January when the sky was cloudy and air as cold as -19°C. In the aquarium, also, the animals huddled together to sleep, regardless of whether they were cold, warm, or hot; under the warmest conditions, both the wild and the captive animals showed signs of heat stress.

In the field, we observed another type of huddling, characteristic of mother-and-calf pairs, which we called "brooding" in as much as it seemed to be of benefit to the calf alone. In this case, there were distinct variations in the degree of contact that seemed to be adaptively related to the weather. For example, we noticed at first that very few calves were in evidence during the chilliest days, but in sunny weather with little or no wind they were frequently seen standing or lying on the ice beside the mother. Subsequently, we discovered that in cold weather the calf was usually situated against the mother's breast, between her forelimbs, and so completely concealed and sheltered that its presence was not detected until the mother became alarmed and began to flee. Calves in this position were estimated to have at least 50 per cent of their body surface in contact with that of the adult. When removed from this maternal shelter and exposed alone to the chilly weather, the calves reacted by seeking protection from the wind, huddling against any warm body or low-conductance material, assuming a "fetal" position, and shivering violently. They were obviously chilled and we concluded that the warmth derived from maternal brooding was an important and, possibly, essential component of their environment. In our experience, weather severe enough to bring about these responses occurred, on the average, in at least three out of four days during the calving season (April-May), and sometimes lasted for ten days at a time.

Posture and fanning. By varying their posture and the position of their appendages, walruses at rest are capable of controlling the amount of exposed surface area. Maximum exposure is attained by sprawling on the back with head and neck extended and flippers outstretched and spread. Minimum exposure is effected by assuming the "fetal" position, with head drawn in, back arched, and flippers pressed tightly against the body. From comparative photographs of one calf in both positions (Plate II), we estimate that the amount of surface exposed in the fetal posture is only about three-fourths as much as in the sprawling posture. That postural regulation of exposed surface is influenced by ambient temperature was determined experimentally. Four newly captured calves, each in a separate wooden crate, were exposed to an in-

crease of 3 or 4°C every 15 minutes. At the lowest temperature, about 1°C, each animal assumed an extreme fetal position with occasional violent shivering. As the temperature was raised, each became more relaxed and paid less attention to keeping its appendages against the body. At 10°C, the animals became fully relaxed and lay either on the back or side; at 15°C they began to sprawl and extend their appendages; at 18°C they became restless and began fanning intermittently with their flippers; at 20°C they were so restless that the experiment was terminated.

The postural adjustments of isolated wild adults in relation to air temperatures were similar to those of the experimental calves. There was clearly a trend to fetal postures at low temperatures (Plate III, fig. 5) and to sprawling at high temperatures, but it was usual to find a wide variety of postures under the latter conditions (Plate III, fig. 6). We found that the fetal posture was almost always assumed when the animals first emerged from the water and was maintained for some time, even when the air temperature was relatively high. In air warmer than 10°C, the emergent animals usually relaxed to a more or less sprawling position after about 30 minutes, or when their skin became dry. We assume that the change in posture reflected a change in the rate of heat loss per unit of surface, i.e., in relation to evaporative cooling.

Fanning by walruses in the aquarium was often seen when ambient temperatures were higher than 20°C but rarely at lower temperatures. In general, fanning animals were visibly hyperemic and hot to the touch, indicating rapid dissipation of body heat. Fanning and superficial hyperemia were seen also in the herds at Round Island, where they were lying in the sun in 13 to 14°C air (Plate IV, fig. 7). We did not see fanning or hyperemia in animals on the ice, even when air temperatures were as high as 7°C, but J. J. Burns (personal communication) saw fanning by some adult males when the temperature was about 8.5°C (Plate IV, fig. 8).

Selection of substrates. A group of three newly captured calves, held in an outdoor pen with a floor of snow, had access to a 1-meter-square piece of plywood and approximately equal areas of canvas and of fresh skin from an adult walrus. The group elected to sleep huddled on the wood, rather than on the snow or other materials, and their persistent use of it indicated that they found it preferable, perhaps because of its lower conductance and specific heat. Pieces of plywood were then provided to several younger calves in separate pens, and

these also were consistently used as beds, in preference to the ice and snow of the pen floor.

A positive response in cold weather to substrates of low conductivity and specific heat was suggested also by the behavior of the captives in New York. When they hauled out to rest in the winter, they clearly avoided snow-covered surfaces, and the female selected a wooden pallet rather than an adjacent concrete platform. The male walrus had only a wooden platform on which to lie.

Probable selection of substrates by free-living walruses was noticed only under the warmest conditions at Round Island. Several times, resting animals were observed to grope about with their hind flippers and, on touching a damp, shaded rock, to press the spread flippers firmly against it, as if aware of its coolness. Although the temperature of the damp rocks in shade was only 1 or 2°C lower than that of the air, they were distinctly cooler to the touch because of their high specific heat and conductivity.

Influence of Weather on Emergence

The opinion that walruses prefer to haul out in sunny weather was expressed by Shulldham (1775, *vide* Allen, 1880:67) and Hayes (1867:404), based on their observations of the animals under natural conditions. We formed the same opinion, independently, from our initial nonsystematic observations of both wild and captive animals and noted, furthermore, that they seemed to stay in the water during windy or stormy weather. The latter was noticed also by Nikulin (1947) and Mansfield (1958:115). These opinions were tested quantitatively by means of a sampling system, in which periodic spot-observations of the activities of captive walruses were recorded by impartial observers and correlated with meteorological data, supplied by the Weather Bureau. Inasmuch as the emergence of the animals and the duration of their exposure to weather might be governed also by regular daily and seasonal cycles of activity, the data were analyzed first for evidence of activity rhythms.

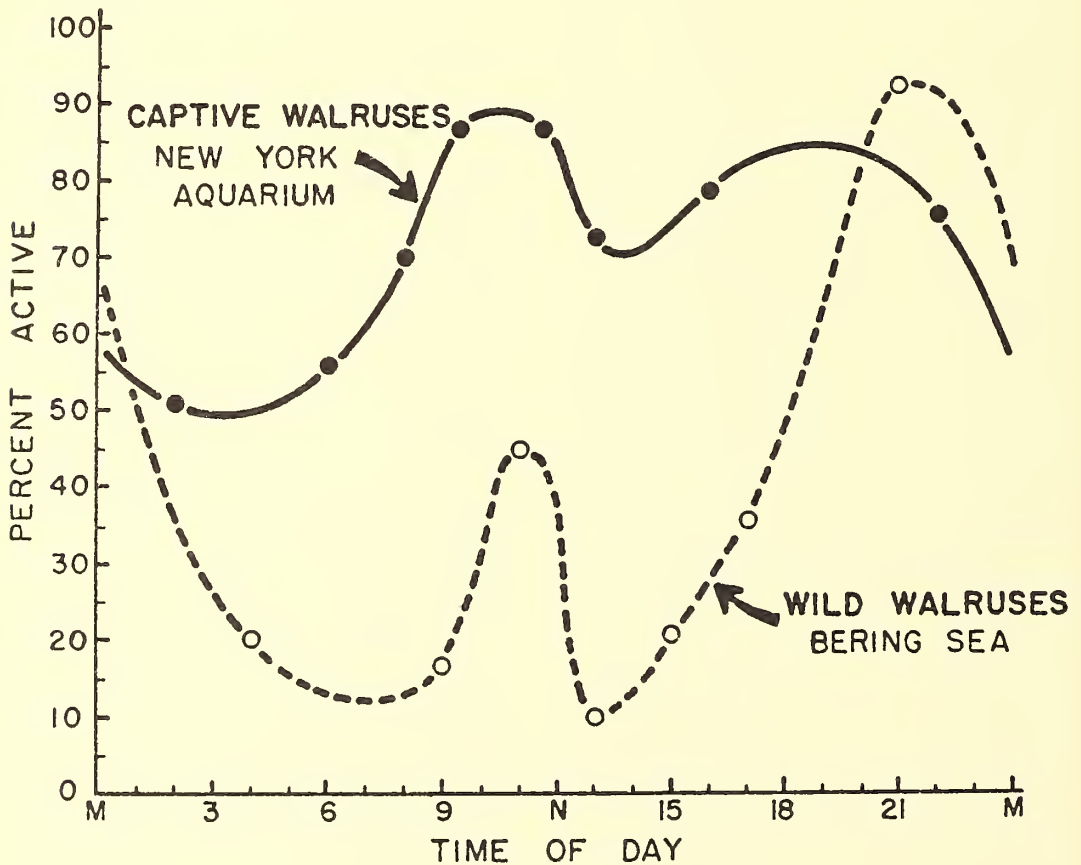
Activity rhythm. Other than an opinion expressed by some Eskimos to Loughrey (1959:39) that walruses feed mostly early in the morning and haul out to rest in the remainder of the day, there is no published information available on the normal alternation of rest and activity in these animals. We obtained an estimate of the mean daily activity rhythm of wild walruses by compiling a series of data on several thousand that were sighted in the Bering Sea in the months of January to June, 1952 to 1960 (F. H. Fay,

K. W. Kenyon & A. Thayer, unpublished). A comparable estimate for walrus in captivity was obtained from more than 1,000 spot-observations of the two juveniles in the New York Aquarium, January to July, 1960. Animals sighted in the water were considered to have been "active;" those sighted on land or ice were considered as "inactive." The relative number of active animals per unit of time was found to show a general circadian rhythm in both the natural and the artificial environments (Text-fig. 2). The animals tended to be most active in the forenoon and evening and to haul out most often in early morning and early in the afternoon. The respective proportions of walrus in and out of the water suggested that the wild animals were less active in the daytime and more active at night than were the captives, perhaps because of differences in their feeding times.

We did not detect any significant changes in

the mean circadian rhythm per month, from January to July, except in the intensity of activity. In both the wild walrus and those in captivity, more time was spent in the water in January than in any other month (Table II). The wild animals were out of the water most often in February and March, at the height of the mating season (Fay, unpublished); the captives were out most in March and April. From April to July, the captives hauled out with increasing frequency at night and decreasing frequency in the daytime.

Activity in relation to weather: captive walrus. Four kinds of meteorological data were utilized for comparison of the weather when the animals were out of the water (inactive) with that when they were in the water (active). These were: air temperature, sky cover (inversely proportional to insolation), precipitation rate and wind velocity (Table III). Since, in a



TEXT-FIG. 2. Comparative patterns of activity rhythms of wild and captive walrus, based on the percentage of occurrences of animals sighted in the water per hour.

TABLE II.
RELATIVE ACTIVITY OF WALRUSES PER MONTH.

Locality and Time	Jan.	Feb.	Mar.	Apr.	May	June	July
Wild walruses, Bering Sea							
Daytime, total sighted	323	261	10124	4569	5891	648	...
Daytime, per cent active	77	4	14	22	29	39	...
Captive walruses, N.Y. Aquarium . .							
Daytime, total observations	46	103	142	122	136	239	149
Daytime, % when active	93	89	74	63	76	79	81
Nighttime, total observations	25	54	57	45	60	59	38
Nighttime, % when active	76	91	75	62	52	59	47

TABLE III.
COMPARISON OF MONTHLY MEAN WEATHER WHEN CAPTIVE WALRUSES WERE *out* OF THE WATER
WITH THAT WHEN THEY WERE *in* THE WATER.

Month	No. of Observations		Mean Temp. (°C)		Mean Daytime Sky Cover ^a		Mean Precip., mm/hr		Wind, 30 mph or More (% Occur.)	
	Out	In	Out	In	Out	In	Out	In	Out	In
January	3	43	2.1	2.4	83	69 ^b	0	.18	0	21
February	11	92	2.2	3.0	81	60 ^b	.13	.43 ^b	27	38
March	37	105	2.7	0.7 ^b	44	58 ^b	.13	.80 ^b	11	19
April	45	77	11.3	10.9	52	59	.29	.42	11	13
May	33	129	15.2	16.5 ^b	56	60	.13	.90	0	8
June	102	259	20.1	21.1 ^b	51	56	.62	.51	2	4
July	74	169	21.8	22.3	41	54	.19	2.86	0	2

^a Expressed as per cent of total sky obscured by clouds; inversely proportional to isolation.
^b P < .05.

preliminary analysis, we found the correlations of activity and weather to be unaffected by the circadian rhythm, all of the data were treated equally. Monthly means were compared by appropriate statistical tests; differences, when $P \leq .05$, were considered as significant. Water temperatures during the six-month period, from mid-January to mid-July, ranged from 4 to 18°C, respectively.

During January and February, the animals stayed in the water most of the time (Table II), and on the few occasions when they did haul out, the weather was slightly cloudier and cooler but less windy than when they were in the water. High winds, 13.4 meters per second (30 mph) or stronger, occurred very frequently in both months and were correlated to a significant degree with the sunniest weather.

March was actually a cooler month than February, though there were more sunny days. The male was out during the day more often than in any other month; the female still remained in the water most of the time. The weather when

either of them was out was warmer, sunnier, drier, and less windy than it was when they were in the water. High winds were still correlated with sunny weather, but they occurred less often than in February.

In April, the female was out of the water more often than the male during the day, and this relationship persisted through July. The daytime weather while either of them was out was slightly warmer and sunnier than when they were in the water, but about equally wet and windy.

By May, both animals were out less frequently during the day and more frequently at night. When they were out of the water in the daytime, the weather was slightly sunnier and less windy, but cooler and drier than when they were in the water. In this and the succeeding month, the high winds occurred with cloudy skies.

The tendency toward hauling out less frequently by day and more frequently by night increased through June and July. In both months, the weather when the animals were out

of the water in the daytime was slightly sunnier; in both the day and the night it was less windy but cooler and about as rainy as when they were in the water.

Consistently, throughout the six-month period, the animals tended to avoid exposure to high winds, irrespective of the other conditions at the time. In addition, they showed a negative response to precipitation, especially in the cooler months, and a consistent affinity for sunshine during March to July, i.e., when it was strong enough to have a distinct warming effect. They evidently were not influenced by "trace" amounts of precipitation, but greater amounts were clearly avoided. Precipitation of 0.5 mm/hr or more occurred about three times more often when they were in the water than when they were out. Neither animal was out of the water in precipitation greater than 0.5 mm/hr except in June, one of the warmest months.

Mean air temperatures when the animals were "out" were at no time greatly different from those when they were "in" the water. The slightly lower temperatures when they were out in January-February apparently were related to the greater sky cover (= less insolation); the higher temperatures when they were out in March-April apparently were related to the lesser sky cover (= greater insolation). From May to July, air temperatures were not correlated with the amount of insolation, and in those months both animals continued to haul out in the sunnier weather but in slightly cooler air than when they were in the water. During sunny days in summer, when air temperatures rose to

25°C or more, they spent most of their time in the water, rarely hauling out for more than an hour at a time. They tended to haul out mostly at night in the warmest months. Though they apparently became acclimatized to a certain degree to the temperate climate, they consistently avoided exposure to the greatest solar and atmospheric heat by escaping to the water.

Activity in relation to weather: wild walruses.

Our data from walruses sighted in the field are less extensive than those from the captives, but they also suggest an avoidance of high wind in cold weather, irrespective of the sky cover (Table IV). In January, all the animals sighted when winds were 4 mps (10 mph) or stronger were in the water, whereas most of those sighted during lower wind velocities were on the ice.

Winds up to 9 mps (20 mph) seemed not to deter the animals from hauling out in air at -7 to 6°C in May, even under overcast skies; indeed, in that month we saw more walruses on the ice in windy weather than when it was calm. In June at Round Island, also, most of the animals resting on a windward beach during a squall with 10 to 12 mps winds and rain (air 12°C) were little affected. Though they were appreciably more restless than they had been earlier in the day in more moderate weather, they showed no clear signs of withdrawing into the sea (10°C). The highest rate of emigration from the beaches of Round Island occurred during the warmest afternoon (air 14°C, wind 0 to 2 mps, sky clear), and we interpreted this as an indication of intolerance of excessive heat, mostly from intense solar radiation.

TABLE IV.
COMPARATIVE WEATHER WHEN FREE-LIVING WALRUSES WERE SIGHTED OUT VS. IN THE WATER
NEAR ST. LAWRENCE ISLAND, BERING SEA.

Month	Animals Sighted		Air Temp. (°C)	Sky Cover	Occurrence of Precip.	Wind Velocity (mps)
	No.	% Out				
January	10	0	-27	clear	none	11-13
January	25	0	-8	clear	none	9
January	11	0	-26	clear	none	4
January	3	33	-23	clear	none	0-2
January	25	100	-19	overcast	none	0-2
January	6	100	-12	overcast	none	0-2
January	25	100	-3	overcast	snow	0-2
March	5	0	-1	clear	fog	0-2
May	310	97	2,3	clear	none	4-7
May	418	87	1,2	clear	none	2-4
May	96	44	-2 to 2	clear	none	0-2
May	58	98	-7 to 2	overcast	none	4-9
May	58	95	-2 to 6	overcast	none	2-4
May	261	90	-5 to 3	overcast	none	0-2
June	3	0	4	clear	none	0-2

DISCUSSION

The physical environment of pinnipeds comprises parts of both the hydrosphere and the atmosphere, with, in some cases, nearly equal amounts of time spent in each. The aquatic portion is usually the more uniformly cold and stable; the atmospheric portion is relatively unstable and heterogeneous and, at times, can be either colder or warmer than the sea. The homeotherm that inhabits both must possess unusual thermoregulatory versatility. Reports from many sources make it clear that this requirement is met in pinnipeds not only by physiological means but by extensive behavioral adjustments as well. For example, in cold or stormy weather, northern fur seals, *Callorhinus*, huddle together or withdraw into the sea (Bartholomew & Wilke, 1956; Fay, unpublished); Weddell seals, *Leptonychotes*, seek sunshine and shelter from the wind (Smith, 1965; Ray & Smith, 1968); gray seals, *Halichoerus*, avoid snow-covered surfaces (Waters, 1965), and Steller sea lions, *Eumetopias*, remain in the water (Kenyon & Rice, 1961). In warm weather, fur seals, *Callorhinus* and *Arctocephalus*, seek shade and moisture, expose areas of bare skin, and fan with their flippers (Bartholomew & Wilke, 1956; Paulian, 1964); monk seals, *Monachus*, make wallows in the damp sand or lie in the shade of a bush or cave (Kenyon & Rice, 1959; van Wijngaarden, 1962); elephant seals, *Mirounga*, and South American sea lions, *Otaria*, may escape the heat altogether by staying in the water (Laws, 1956; Vaz-Ferreira & Palerm, 1961). Some of these tactics may considerably extend the thermal comfort zone well beyond the capacity of physiological mechanisms alone; others, such as escape into the water, indicate that the limits of the comfort zone have been exceeded.

We assume that adult walruses, like other polar pinnipeds (Irving & Hart, 1957; Davidov & Makarova, 1964), are fully adapted for thermoneutral existence in icewater, even while at rest, for they spend the greater part of their life there and may remain immersed for several days or weeks at a time. They are capable of sleeping in the water and frequently do so, yet at certain times they seem more inclined to rest in air than in the ostensible comfort of the sea. While out of the water or in anticipation of hauling out, they are notably selective of weather conditions, generally seeking exposure to sunshine and avoiding exposure to high winds and precipitation. In addition to their selection of the more favorable thermal conditions, usually warmer than the sea, they employ heat-conserving behavior in all but the warmest weather. The usual result is a relatively high, stable temperature

in the skin and appendages (Ray & Fay, 1968), and we think that this is the principal benefit derived from hauling out. The tissue most affected by it is the epidermis, the outermost layer of the skin. Whereas, it is about as cold as the water during immersion, it can become 30°C warmer following emergence. Since epidermal mitosis in pinnipeds probably occurs only at relatively high tissue temperatures (Feltz & Fay, 1967) and, perhaps, only when the animals are inactive or asleep (Bullough, 1962; Bullough & Rytömaa, 1965), growth and regeneration of the skin, as in the molt and healing of wounds, may be feasible only when the animals are at rest out of the water. This is not a new theory (Laws, 1956; McLaren, 1958), but it is presented here in a new context, with new support. We feel that it could help to explain the conservative, thermophilic behavior of walruses and other polar pinnipeds when in air, in contrast to their apparent comfort in the usually colder sea.

The principal behavioral adjustments of walruses that favor the conservation of body heat when at rest in air are huddling, fetal posture, and basking in the sunshine. Huddling may have special significance for the calves, which possess less than half as much physical insulation (hair and blubber) as other arctic pinnipeds of comparable size. For the first two or three months after birth, thermal compensation for their deficiencies seems to be derived principally from contact with their mother ("brooding"). We consider brooding by walruses as the behavioral analogue of the woolly coat of young phocid seals, in that it provides warmth and insulation for the young animals while their blubber layer is developing (Davydov & Makarova, 1964; Ray & Smith, 1968). The young walrus also remains mostly in the atmosphere during this critical period, and the mother remains there with it. On many occasions, we observed that the cows with very young calves were extremely hesitant to take the calves with them into the cold water when threatened by hunters, whereas those with older calves showed virtually no hesitancy at all.

The huddling of adult walruses at rest has been recognized in a general way for a long time, but its potential contribution to thermal economy evidently has not been considered before. Among the Pinnipedia other than walruses, gregariousness is common during the pupping, mating, and molting periods, but huddling is uncommon. It seems significant that the walrus, the most polar of the otarioid seals and the most sparsely haired of all the pinnipeds, is also the most thigmothermal. By extensive mutual reduction of surfaces exposed to the cold air and substrate, the huddling walrus herd becomes a

heat-exchanging and heat-conserving unit with an advantage for arctic living. However, the persistence of thigmotactic behavior under all thermal conditions may place a limit on the amount of climatic heat that can be tolerated. Huddling is disadvantageous in warm weather, for it severely obstructs the dissipation of heat from the body.

By changing posture, the walrus is capable of regulating the amount of exposed surface and, thereby, of controlling the rate of heat loss. In contrast to huddling, posture is adjusted according to the ambient thermal conditions. The fetal posture (minimal exposure of surface) is clearly a reaction to cold that has potential value for conservation of body heat, whereas sprawling, with extension of the appendages, undoubtedly helps to accelerate cooling by exposing the greatest surface area for dissipation of heat. When very warm, walruses increase the convective heat loss from their body by fanning, usually with one or both of the foreflippers. These are small relative to body size but have a large surface-to-volume ratio and can accommodate a large volume of blood probably at a high flow rate. The capacity of the hind flippers for transferring heat to the environment is enhanced also by evaporation when they become wetted by the animal's watery excrement. We frequently noticed also that the fore and hind flippers were damp in the absence of any extrinsic supply of moisture, but we were unable to determine the source of the dampness. Sweat glands were not found in any tissues from the bare flippers, though they were abundant in skin from the hairy parts of the body (Fay, unpublished).

Basking is another effective means for conserving body heat, largely by acquiring heat from solar radiation. We assume that the dark surface of the walrus' body absorbs radiant heat about as well as a black body, and that the short hair serves to retain it somewhat better than a bare surface. The hair may function also as a baffle, protecting against excessive convective heat loss in all but the windiest weather.

Walruses in captivity at mid-latitudes showed an affinity for sunshine from March to July but tended to avoid prolonged exposure during the warmest months, when the insolation was about twice as strong as that in their native habitat. The calves were more inclined to expose themselves to it than were the juveniles, perhaps because of their smaller size and less effective thermoregulatory system. However, we observed, as did Reventlow (1951), that their

greater exposure seemed to be the cause of a granular condition of the skin, tentatively identified as solar keratosis (cf. Mackie & Mackie, 1963). This occurred during the molt, in June, after the hair was shed and the skin was unprotected from the direct rays of the sun. In our animals, an acne-like condition often occurred with it, possibly due to blockage of the sebaceous ducts by an excess of keratin (van Scott, 1959).

The ultimate behavioral response to thermal conditions of the atmosphere is withdrawal into the water ("escape"). With increasingly cold weather, escape is preceded by the extreme fetal posture and intense shivering; with increasing warmth, it is the normal successor to sprawling and fanning. We believe that the range of conditions under which escape does not occur includes but slightly exceeds the "comfort zone." That is, we think that escape is not induced until the animals become uncomfortably hot or cold. Walruses that were acclimated for a year or more to the temperate climate of New York showed the escape reaction mostly when air temperatures were lower than 0°C or higher than 25°C, given sunshine, light winds, and a wet concrete substrate on which to rest. Newly captured calves, on a dry, wooden substrate in shade, were comfortable in still air only at temperatures between 5 and 18°C, and even after acclimation to warm weather in New York for 2 weeks, they tended not to lie out in air warmer than 20°C. Wild adults on ice may occasionally tolerate air as cold as -35°C with strong winds (Freuchen, 1935), but in our opinion, this is more the exception than the rule. Whereas the majority of those seen by us were on ice when air temperatures were higher than -20°C with little or no wind, nearly all were in the water when the air was colder or the winds were stronger. The upper threshold of air temperature that induces wild adults to escape or remain in the water seems to be between 10 and 15°C, given sunshine, light winds, and a damp, rocky substrate or ice.

SUMMARY AND CONCLUSIONS

1. The influence of climate on the distribution of walruses was investigated by observing their behavioral reactions to weather in the natural arctic and subarctic environment and in the temperate climate at the New York Aquarium. Walruses spend a large proportion of their time out of the water and are, therefore, exposed to conditions of the atmosphere nearly as often

as to those of the hydrosphere. Whereas they can sleep in the water in apparent comfort, they usually haul out on ice or land to sleep, especially during the spring and summer.

2. When at rest out of the water, they are highly gregarious and tend to huddle together at all times. This mutual reduction of exposed surface is advantageous for conservation of heat in cold weather, but it is a deterrent to their hauling out or remaining out when the weather is warm. Exposure of surface area is regulated also by the sleeping posture, which is adjusted for minimal exposure in cold and maximal exposure in warm weather.

3. Walruses are most active in the water at night and generally haul out to rest in the daytime. In doing so, they usually seek exposure to sunshine and avoid high winds and heavy precipitation. Their tolerance of wind and precipitation increases with rising air temperatures and increasing insolation, while their affinity for sunshine seems to remain unchanged. However, they evidently cannot tolerate for long the intense solar radiation in summer at mid-latitudes, and the young may be adversely affected by it.

4. The principal benefit derived from their hauling out to sleep seems to be the warming of their peripheral tissues, which may require heat and physical inactivity to fulfill their growth and reparative functions. Sustained warmth of the skin and appendages may be especially important for the molt, healing of wounds, and the development and survival of the newborn young.

5. When the weather is excessively cold or hot, the animals withdraw into the relative comfort of the sea after brief exposure or refrain from hauling out altogether. Thus, the upper and lower limits of their thermal tolerance are recognizable from this escape reaction. These limits may be expected to vary seasonally and, perhaps, with age, sex, reproductive status, health, and individuality.

6. The average limits of thermal tolerance of adult Pacific walruses while at rest in air seem to be between -20 and $+15^{\circ}\text{C}$, given light winds, moderate insolation, and a cool, damp substrate on which to lie. Colder and warmer conditions may occasionally be tolerated, but only for short periods.

7. The highest air temperatures and most intense insolation received in coastal areas at the

southern edge of the Pacific walrus' present range tend to induce the escape reaction. Warmer conditions, such as are found farther to the south, could be expected to discourage them to a greater extent from hauling out during the day in the spring and summer months, when they would ordinarily spend the most time out of the water. We feel that the conflict with their normal feeding, molting, and calving schedules could be sufficient to deter them from extending their range southward under present climatic conditions.

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EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. Herd of adult female walruses resting on an ice floe off Cape Lisburne, Alaska, summer, 1937. Photo by M. Woodbridge Williams.
- FIG. 2. Herd of male walruses resting on Round Island, Bristol Bay, Alaska, June 27, 1958. Photo by Karl W. Kenyon.

PLATE II

- FIG. 3. Walrus calf resting in "fetal" position with near minimum exposure of body surface. New York Aquarium, June 18, 1961.
- FIG. 4. Same calf, a few minutes later, in sprawling position with near maximum exposure of body surface and appendages. Note huddling calves in background.

PLATE III

- FIG. 5. Adult female walrus sleeping in the "semi-fetal" position. St. Lawrence Island, Alaska, May 16, 1959. Air temperature at

the time was 3.5°C, the wind about 7 mps, and the sky was clear.

- FIG. 6. A group of male walruses that had recently emerged from the water, Round Island, June 27, 1958. Note fetal posture of the animal at center. Air temperature 13°C, wind 1 mps, sunny with a high, thin overcast. Photo by Karl W. Kenyon.

PLATE IV

- FIG. 7. Herd of male walruses resting in the afternoon sun, Round Island, June 24, 1958. Note the animal sprawled on the rock at center and the abundance of outstretched flippers, many of them fanning (arrows). Air temperature 14°C, wind about 1 mps, sky clear. Photo by James W. Brooks.
- FIG. 8. Two male walruses resting in the sprawling posture with flippers extended and spread, Bering Strait, May 18, 1963. The animal at left was fanning. Air temperature 8.5°C, wind calm, sky clear. Photo by John J. Burns.



FIG. 1



FIG. 2

THE INFLUENCE OF CLIMATE ON THE DISTRIBUTION OF WALRUSES, *ODOBENUS ROSMARUS* (LINNAEUS). I. EVIDENCE FROM THERMOREGULATORY BEHAVIOR.



FIG. 3

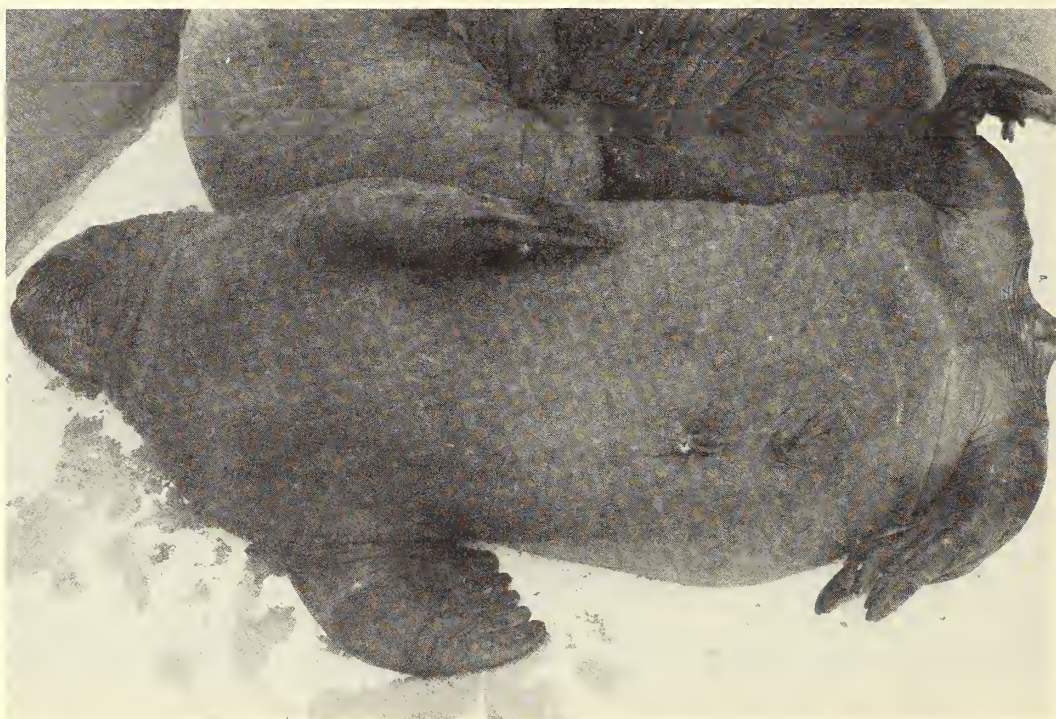


FIG. 4

THE INFLUENCE OF CLIMATE ON THE DISTRIBUTION OF WALRUSES, *ODOBENUS ROSMARUS* (LINNAEUS). I. EVIDENCE FROM THERMOREGULATORY BEHAVIOR.



FIG. 5

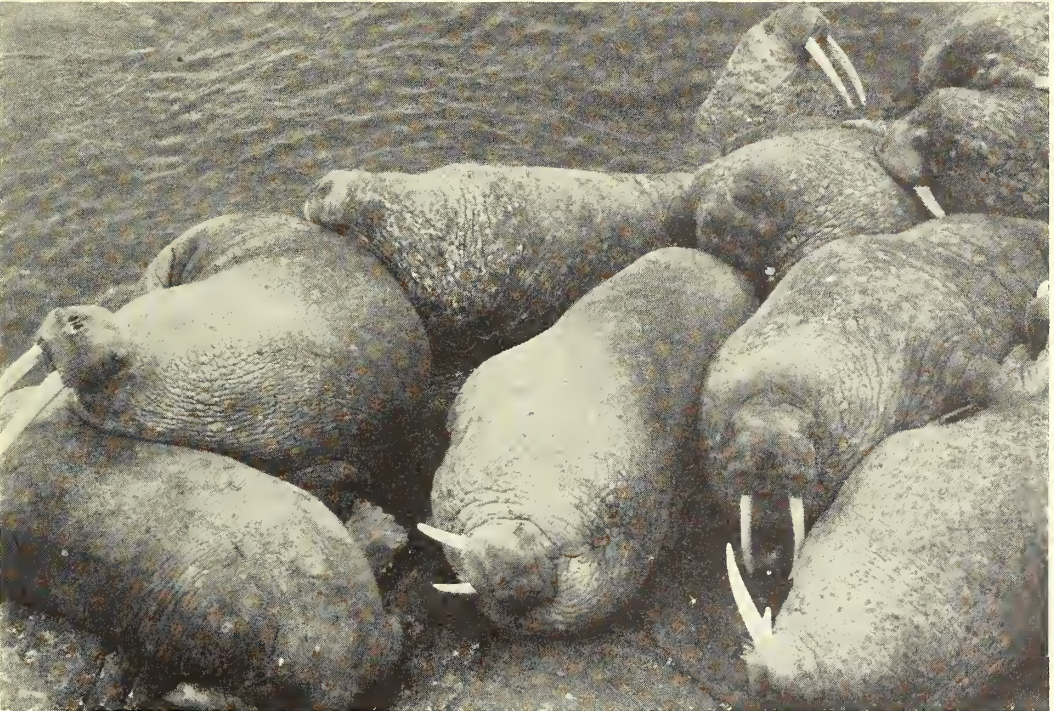


FIG. 6

THE INFLUENCE OF CLIMATE ON THE DISTRIBUTION OF WALRUSES, *ODOBENUS ROSMARUS* (LINNAEUS). I. EVIDENCE FROM THERMOREGULATORY BEHAVIOR.



FIG. 7



FIG. 8

THE INFLUENCE OF CLIMATE ON THE DISTRIBUTION OF WALRUSES, *ODOBENUS ROSMARUS* (LINNAEUS). I. EVIDENCE FROM THERMOREGULATORY BEHAVIOR.

2

Influence of Climate on the Distribution of Walruses, *Odobenus rosmarus* (Linnaeus). II. Evidence from Physiological Characteristics.

CARLETON RAY¹ AND FRANCIS H. FAY²

(Text-figures 1-9)

INTRODUCTION

THE principal objective of this and the foregoing study (Fay & Ray, 1968) was to test the theory first expressed by von Baer (1838) that walruses are prevented by warmer climates from extending their range southward. The rationale was that walruses are closely adapted to the environment they occupy; that they are highly mobile and could readily move farther southward; that no physiographic barriers prevent them from doing so, therefore they must be inhibited by nonadaptation to some physical or biotic factors of the more southerly environments. Upon comparing the principal physical and biotic characters of their range with those of areas immediately to the south, we concluded that climate was the most probable restrictive factor. We and others have observed that, under certain conditions, walruses and some other pinnipeds seem to be sensitive to extremes of atmospheric and solar heat.

The influence of climate on the distribution of animals has usually been evaluated indirectly by correlating climatological data with the altitudinal or latitudinal range of species (see review by Allee, *et al.*, 1949). We have taken a more direct

course by examining the specific reactions of individual animals to climatic and microclimatic conditions. Walruses are adapted to the water of the polar sea, which in terms of cooling power is one of the coldest environments on earth. That they are highly efficient at conservation of body heat is indicated by their ability to sleep in the cold water. However, they also spend a large part of their time out of the water, where they are exposed to a greater variety of thermal conditions, the warmest and coldest of which evoke behavioral signs of thermal stress, considered in our previous paper. In this paper we report some physiological responses associated with the observed behavior.

The physiological thermoregulation of pinnipeds has been studied in recent years principally by Irving and associates (Irving, *et al.*, 1935; Scholander, 1940; Scholander, *et al.*, 1950a, 1950b; Irving & Hart, 1957; Hart & Irving, 1959; Irving, *et al.*, 1962), largely using restrained animals to facilitate measurement of physiological characteristics. These animals were exposed mostly to controlled environments, adequately described by ambient temperatures alone. The results indicated the animals' capability for maintaining a constant internal temperature exclusively by physiological means, but they did not describe the total thermoregulatory responses of the free-living animal nor take into consideration the complex thermal conditions of the natural environment.

In this study, we worked mostly with animals that were free to react to weather in their natural environment or in their quarters at the New York

¹Department of Pathobiology, School of Hygiene and Public Health, The Johns Hopkins University, Baltimore, Maryland. Formerly, Curator, New York Aquarium, New York Zoological Society, Coney Island, New York.

²Biologist, Arctic Health Research Laboratory, Public Health Service, U.S. Department of Health, Education, and Welfare, College, Alaska.

Aquarium. In doing so, we hoped to gain insight into the interrelationships of behavior and physiology in thermoregulation, particularly as they interact near the upper limits of the "tolerance zone." This zone is defined as comprising the range of weather conditions tolerated by pinnipeds while at rest in air. When its limits are exceeded, the animals withdraw to the water (Fay & Ray, 1968).

MATERIALS AND METHODS

The wild animals studied were 14 adult and subadult Pacific walruses, *O. r. divergens* (500 to 1560 kg), in the vicinity of St. Lawrence Island, Bering Sea, and Round Island, Bristol Bay, Alaska. Data on captive animals were obtained from a juvenile male Atlantic walrus, *O. r. rosmarus* (age four to five years, weight 500 to 600 kg), and a young female Pacific walrus (age one month to two years, weight 54 to 254 kg) at the New York Aquarium. Data from calves were obtained from 11 newly captured animals (ages one day to two months, weights 59 to 73 kg) at Gambell, Alaska, at the Woodland Park Zoo in Seattle, and at the New York Aquarium, Coney Island, New York.

All data from wild adults and subadults were obtained from animals that were at rest when killed by rifle, mostly during the course of an Eskimo hunt. Data from juveniles and calves were obtained on living animals while they were at rest and free to respond behaviorally to the ambient conditions. Rectal temperatures were taken at depths of 15 to 20 cm with mercury rectal thermometers or Weston dial thermometers that had been standardized at 37°C. All other temperatures were taken with the latter. Subsequent checks against telethermometers (YSI) showed close agreement with Weston thermometers, the chief difference being time to reach equilibrium. Body skin temperatures were

measured on the lateral, ventral, or dorsal aspect, whichever was driest and most distant from the substrate. Flipper temperatures were taken on the webbing of the rear flippers about midway between the tarsals and the tip.

Breathing and heart rates were counted on resting animals, mostly coincident with measurements of skin temperature. Breathing was observable by nostril action, sound, or chest inflation. Heart action was detected visually or by axillary palpation.

Data from wet and dry animals were treated separately. In all cases, ambient weather was recorded at the site and level of the animal and at the same time as physiological or behavioral observations.

RESULTS

Internal Temperatures

The mean body core temperature (thoracic cavity) of ten subadult and adult walruses in an ambient temperature range of -1 to 14°C was 36.6°C, or about 1.2°C lower than the mean for terrestrial mammals of a similar size (Morrison & Ryser, 1952). Rectal temperatures of the same walruses were nearly identical to the core temperatures (Table I). The rectal temperatures of calves were significantly higher than those of the subadults and adults, averaging 37.5°C. Some of the highest temperatures were measured in teething calves in temperate climates, and it is conceivable that temperatures were elevated as a result of that condition. We also suggest that the warmer conditions of captivity induced higher rectal temperatures, but our data from calves in cold conditions are too few to show this. A diurnal fluctuation of body temperature also was suggested. The mean rectal temperature of five calves in midmorning was $38.2 \pm 0.29^\circ\text{C}$, whereas in the same calves in late afternoon it was $37.8 \pm 0.18^\circ\text{C}$.

TABLE I
INTERNAL TEMPERATURES OF RESTING
WALRUSES AT AIR TEMPERATURES OF -1 TO 25°C

Age of Animals	No. Observations	Thoracic Temperature °C		Rectal Temperature °C	
		Range	Mean \pm S.E. _m	Range	Mean \pm S.E. _m
1-6 months	36	35.3-39.0	37.5 ± 0.13
	1	37.0
1-3 years	1 ^a	36.2
> 5 years	10	34.0-38.0	36.2 ± 0.42
	10	34.0-38.0	36.6 ± 0.32

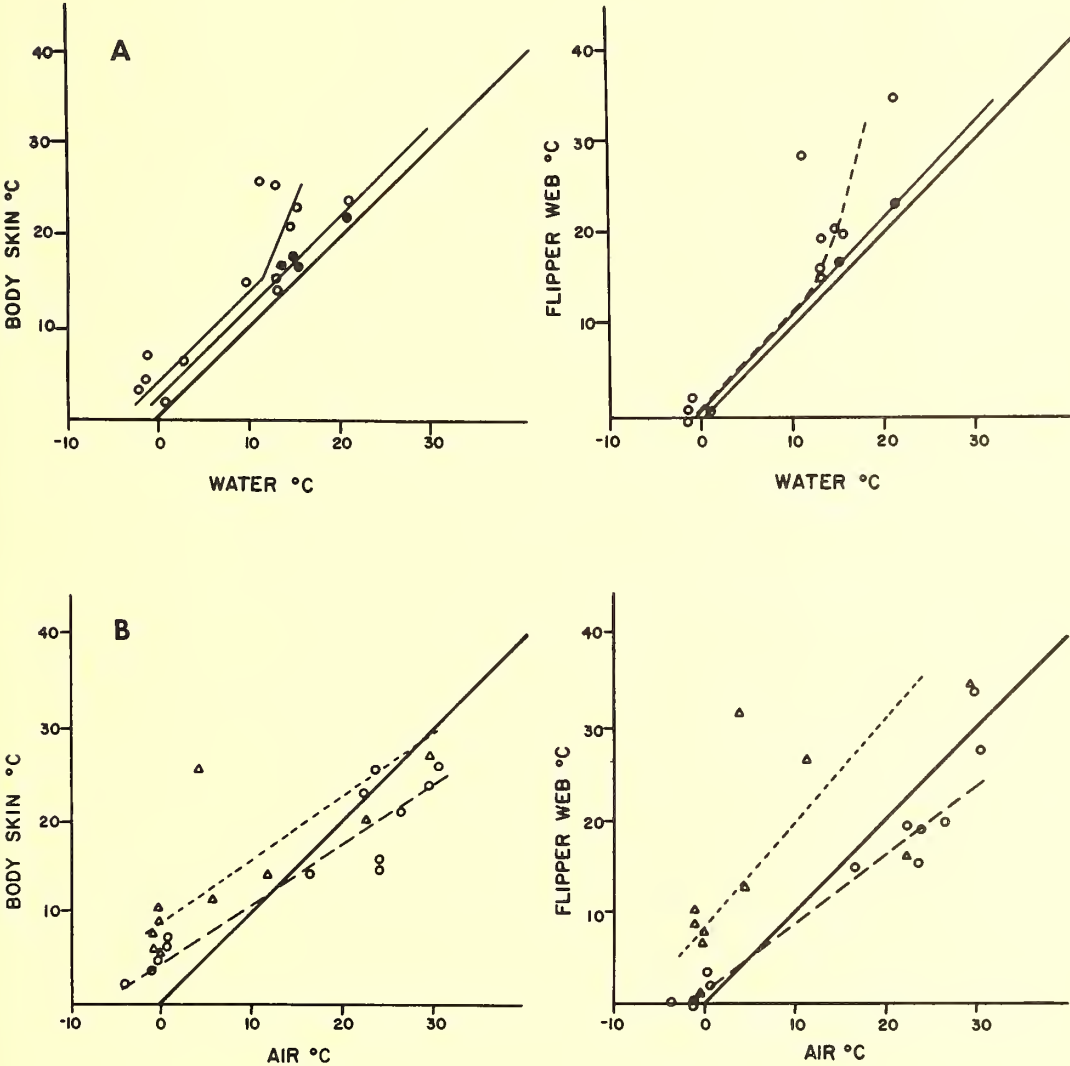
^aData from Rausch, unpublished.

Temperature of the Skin When Wet

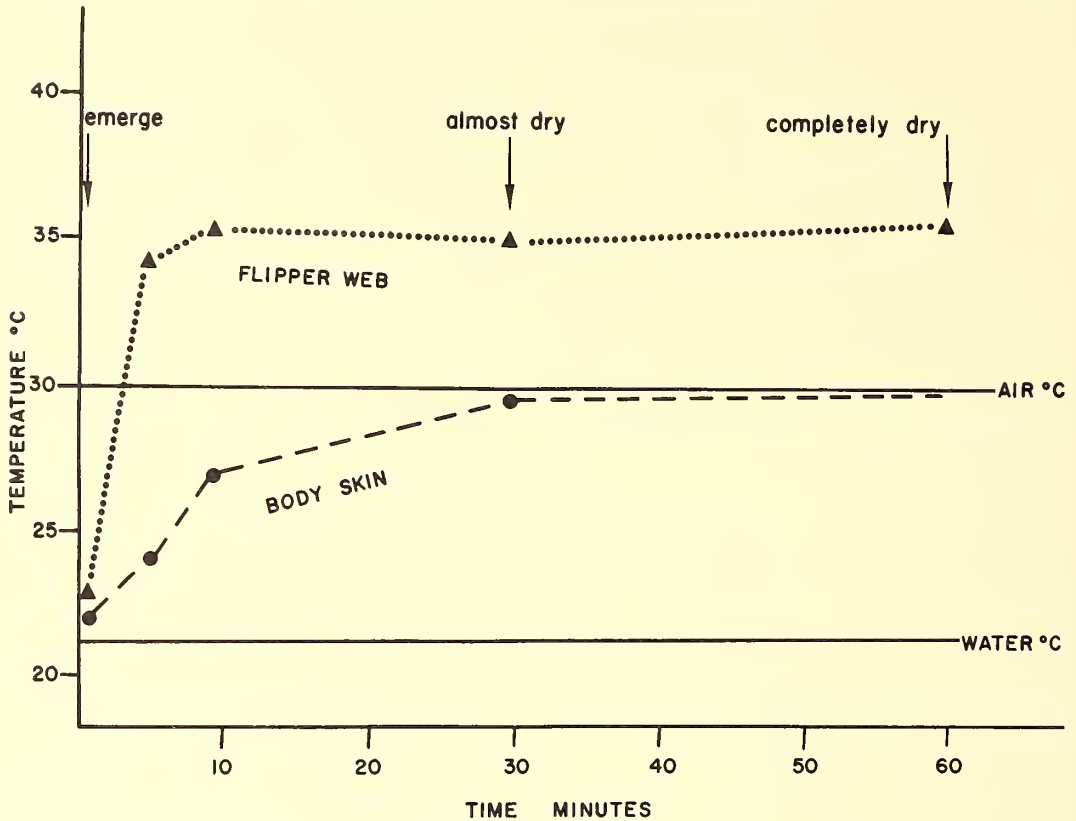
The body surface and flippers of moderately active animals during immersion were 1 to 3°C warmer than the water (Text-fig. 1A). This finding is in accord with those of other workers (Irving & Hart, 1957; Hart & Irving, 1959; Ray & Smith, 1968) and indicates that, whether restrained or not, pinnipeds are usually about as cool on the body surface as the water in which they are immersed.

For at least five to 10 minutes after emerging

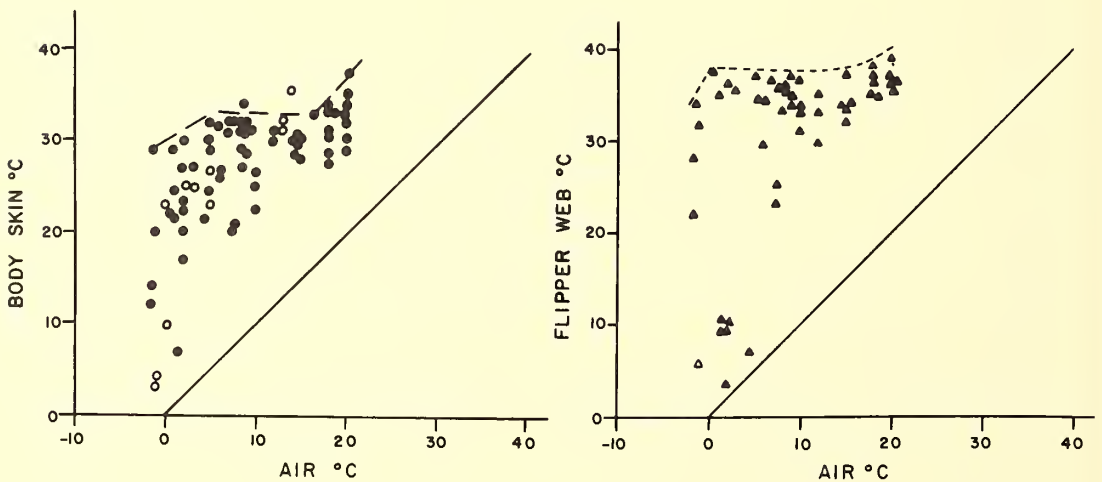
from the water, the walruses remained cool on the body surface, usually within 8°C of the water temperature, provided that the water was cooler than 10°C and the air cooler than 20°C. The body surface warmed more rapidly when air and water temperatures were high, and the temperature of the flippers rose faster and more erratically than did that of the body skin (Text-fig. 1B). Within an hour after emergence, the skin of the body and flippers was usually dry and had attained a relatively stable temperature, most



TEXT-FIG. 1. Temperatures on the skin of the body and rear flipper web of walruses: (A) in water —●— and immediately after emergence into air —○—. (B) in air within 10 minutes —○— and within 20 minutes ---△--- after emergence.



TEXT-FIG. 2. Example of the rate of warming of the body skin and rear flipper web of a captive juvenile female walrus from the time of emergence into air until the skin was dry.



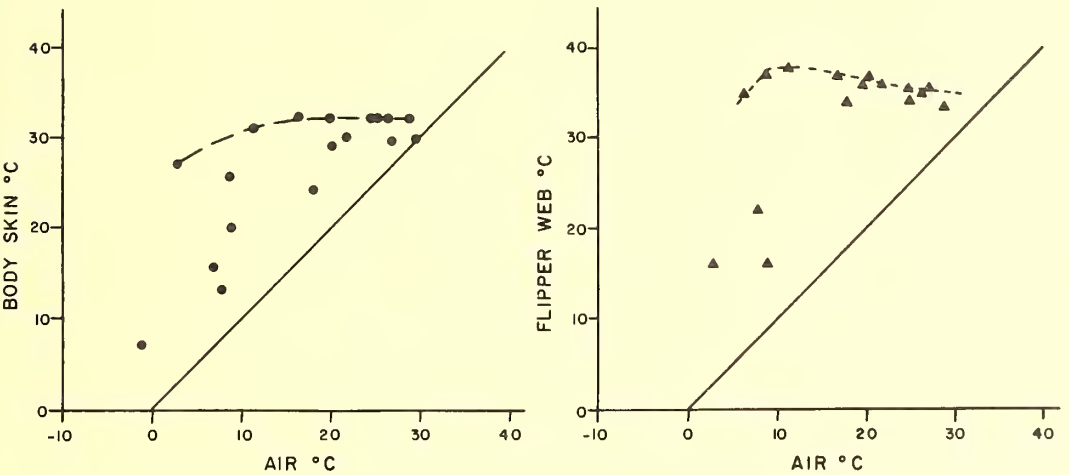
TEXT-FIG. 3. Temperatures of the dry skin of the body and rear flipper web of newly captured calves and wild adult walrus at rest in air. ● ▲ = newly captured calves. ○ △ = wild adults. Curves delimit the usual upper limits of temperature.

often higher than that of the air. The role of the flippers in the dissipation of heat is indicated by the high temperatures attained by them, especially in air warmer than body skin temperature. (Text-fig.2).

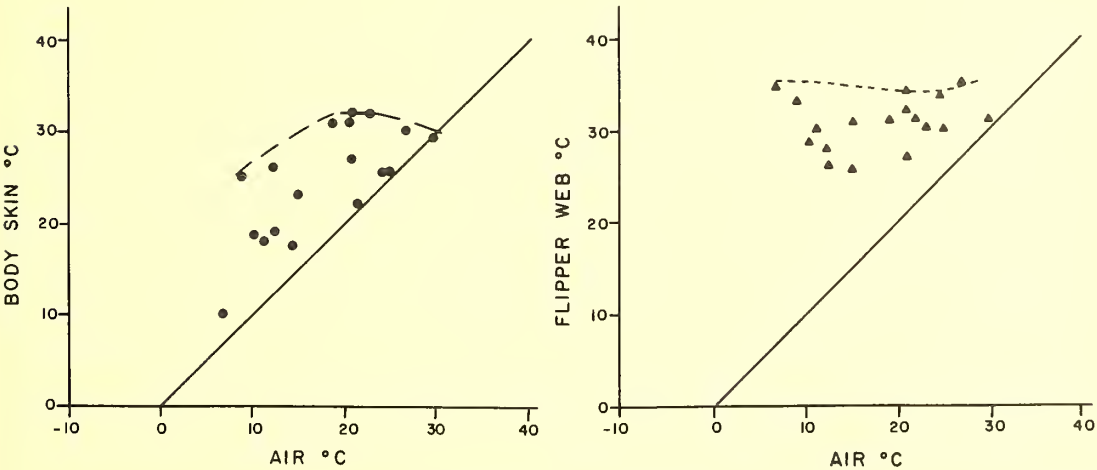
Temperature of the Skin When Dry

At air temperatures from 0°C, to about 15°C, the temperature of the dry skin on the body of wild calves and adults was usually higher than 20°C but rarely higher than 32°C (Text-fig. 3). The latter seemed to be an upper "limit," beyond which the skin temperature ordinarily did not rise. Thus, the skin/air temperature curve of

wild walruses flattens out to a "plateau" in the range from near freezing to about 15°C; at higher air temperatures, the curve again rises steeply. This plateau was evident also in the captive walruses at the New York Aquarium, within a higher range of ambient temperatures (Text-figs. 4-5) and has not been noticed previously in pinnipeds, perhaps because it does not occur in restrained animals or occurs in them over a narrower range of ambient temperatures (cf. Irving & Hart, 1957). It was detected recently in unrestrained Weddell seals (Ray & Smith, 1968), and we have also observed it in other unrestrained pinnipeds at rest (unpublished). Eleva-



TEXT-FIG. 4. Temperatures of the dry skin of the body and rear flipper web of a juvenile female walrus at the New York Aquarium. Curves delimit the usual upper limits of temperature.



TEXT-FIG. 5. Temperatures of the dry skin of the body and rear flipper web of a juvenile male walrus at the New York Aquarium. Curves delimit the usual upper limits of temperature.

tion of skin temperature above the 32°C plateau coincided in calves and adults with the first behavioral signs of heat stress (Fay & Ray, 1968).

Under most conditions, the flippers were somewhat warmer than the surface of the body and showed an even greater tendency for sustained high temperature over a wide range of air temperatures (Text-figs., 3-5). In air warmer than 0°C, the flippers were usually between 30 and 37°C; they were cooler than 25°C only when wet or in contact with ice or snow. Brief, spontaneous fluctuations of 5 to 6°C in flipper temperature were detected at ambient temperatures lower than 10°C, and fluctuations of 2 or 3°C were occasionally detected at higher air temperatures.

The temperature of the calves' flippers rose above the 37°C level only in air warmer than about 15°C, i.e., at or about the same ambient temperatures in which the skin of the body exceeded the 32°C plateau and signs of heat stress first appeared. The occurrence of flipper temperatures of 38 and 39°C might have been indicative of rising internal temperature, such as could occur with increased metabolism or inadequate dissipation of heat.

Calves resting in air warmer than 15°C and adults in air warmer than 10°C showed a distinct reddish cast on the body and flippers, in contrast to the normal pallor of animals under cooler conditions. Pale adults killed when the air was -20 to 5°C were usually cool to the touch and their skin and flippers scarcely bled at all when slashed. Reddish adults killed in air of 13 to 14°C were contrastingly hot to the touch and bled profusely when slashed. When these hot animals were thoroughly bled out, their skin became as pale as the cool animals', demonstrating that the redness and heat were due to vasodilation and the resulting hyperemia. This hyperemic condition has often been called sunburn in popular literature.

The contrast between hyperemic and ischemic animals was especially noticeable at Round Island, where most of the animals were in a nearly hairless stage of their annual molt. When in the 10°C water, the lightly pigmented adults appeared nearly white, whereas they became reddish after lying out on the beach for an hour or more. When these reddish animals were chased back into the water, their skin at once regained its pallor.

Breathing and Heart Rates

Both breathing and heart rates appear to be highly variable, even in resting calves. Minimum breathing rates in calves exposed to stepwise increases of still air temperature in shade declined from 16 per minute at -1°C to 4 per minute at

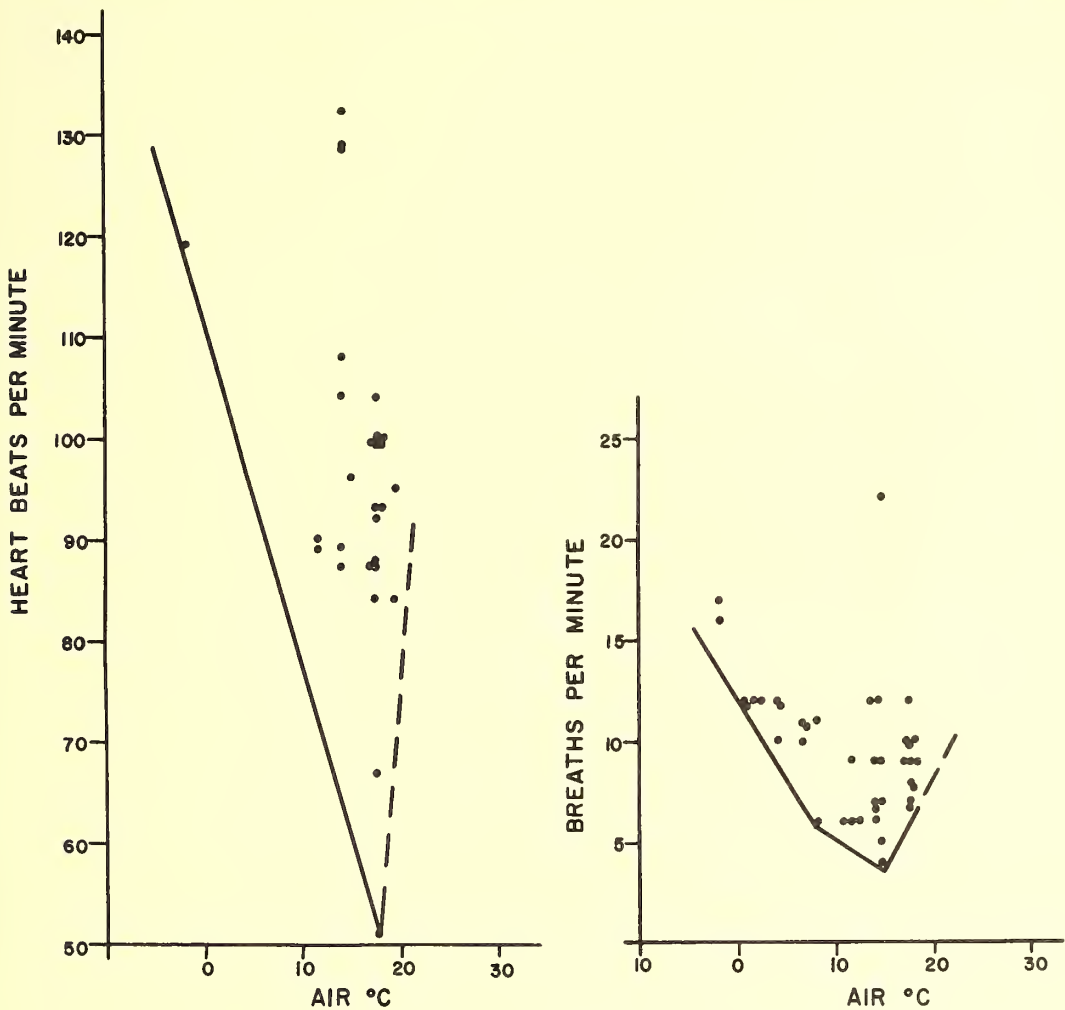
15°C, and rose again to 7 per minute at 18°C (Text-fig. 6). These rates include brief periods of apnea, especially prevalent at 10 to 18°C, and each point in the graph represents the mean of several counts. We did not notice panting under any conditions. Minimum heart rates in the same animals declined from 119 to 52 per minute in the same temperature range, though rates as high as 133 per minute were recorded at about 15°C. Lacking any special equipment for measuring heart rates, we were usually unable to determine them at ambient temperatures lower than 5°C or even 10°C due to the animals' frequent violent shivering. Since these were animals destined for display at the aquarium, we did not expose them to temperatures higher than 19°C, at which they already appeared distressed.

Temperature Gradients in the Skin and Blubber

Temperatures of the tissues were measured at several depths up to 20 cm in a few adults immediately after they were killed. Some of these animals were dry and on land or ice; others were wet and on ice. Relatively steep temperature gradients were indicated in most cases, and these were taken up mainly in the skin and blubber (Text-fig. 7). Their lengths, taking the inner end point to be 0.5°C lower than the deep thoracic temperature (Irving & Hart, 1957), ranged from near 0 cm to about 15 cm. Compared with the gradients measured in smaller pinnipeds (Hart & Irving, 1959), these were much longer and were not correlated in the same way with the internal temperature-skin temperature difference. We assume that these dissimilarities were due to the greater thickness of the walrus' skin and blubber, which should be expected to accommodate a longer gradient if the tissues are effective as insulation.

The shortest gradient amounted to virtually no gradient at all. This was measured in an adult male lying on a rocky beach in sunshine when the air was 14°C (Text-fig. 7I). The surface and cutaneous tissues of this specimen were about as warm as the interior of its body. Under similar conditions but without sunshine, two other adults had surface temperatures 5 to 7°C lower than that of the body core (Text-figs. 7G, H). We attribute the greater superficial warmth of the first animal to solar radiation. For example, a mercury thermometer and a Weston dial thermometer exposed to the sun registered 22 and 34°C, respectively, and the surface of a walrus cadaver nearby was 40.5°C. Thus, the length of gradient is not purely a function of air temperature.

We were not equipped to measure temperature gradients in the living calves and had no opportunities otherwise to determine the form of



TEXT-FIG. 6. Heart and breathing rates of newly captured walrus calves with relation to ambient still air temperature in shade.

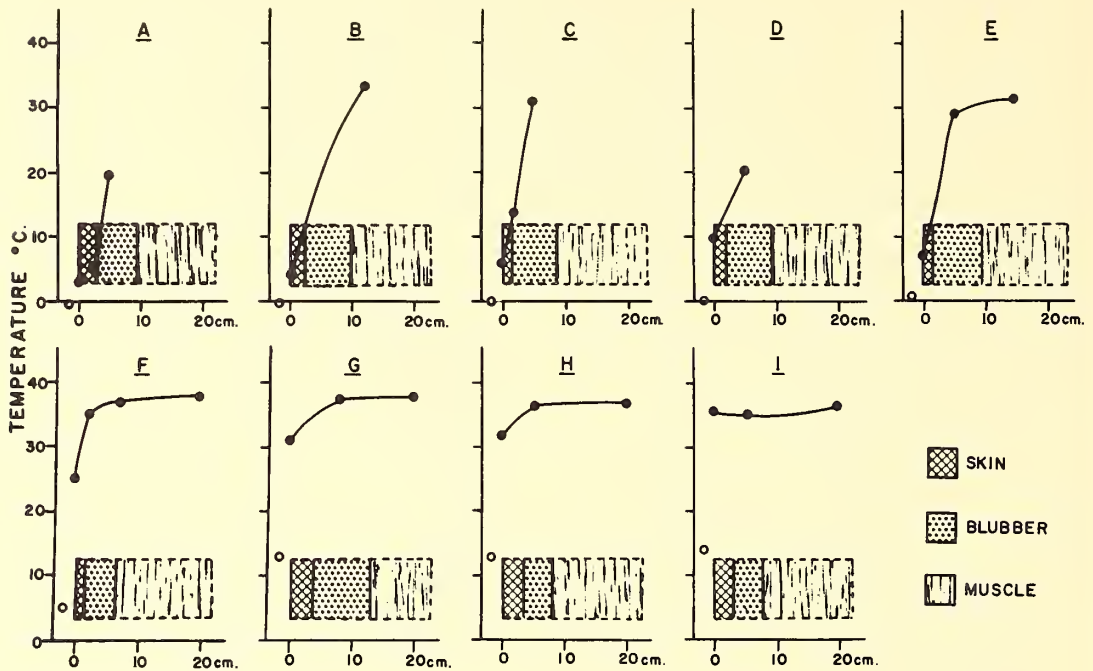
such gradients. Although the calves were about twice as large as young harbor seals, such as those used by Irving and Hart (1957), the thickness of their insulation (skin and blubber) was about the same. Therefore, we assume that the temperature gradients in their tissues were comparable to those of the seals, since gradient length seems to be as much a function of the thickness of the insulation as of the internal temperature-skin temperature difference.

DISCUSSION

Correlation of Thermoregulatory Behavior and Physiology

The walrus is a homeothermic mammal with an internal temperature of about 36.6°C, probably intermediate between those of other small-

er and larger pinnipeds (Bartholomew, 1954; Bartholomew & Wilke, 1956). We assume that this temperature is maintained in a balance between heat production and heat loss and that the production of metabolic heat is usually at the basal level in resting walruses, whether in or out of the water. The loss of heat is closely regulated by vasomotor and behavioral means, within the limits imposed by the animal's surface-to-volume ratio and amount of physical insulation (hair, skin, and blubber). We have described in the previous paper the behavioral adjustments that walruses make in response to their thermal environment, and we report here some indices of their physiological adjustments. Most of our information was obtained from very young animals, up to one or two months old. From their behavior alone, it was clear that these infants



TEXT-FIG. 7. Temperature gradients in the superficial tissues of adult wild walrus within a few minutes of death. Skin and blubber thicknesses at the site of measurement are drawn to scale (thinner-skinned animals are females). Air temperatures within 1 meter of the body are indicated by open circles to the left of each section. A-D were wet and E-I were dry animals.

were not yet fully adapted to even the moderate cold of the arctic springtime, but that they had about the same tolerance of heat as the adults. By correlating their physiology and behavior (Text-fig. 8), we obtained a useful model with which the adults' reactions could be compared.

The calves resting in air at -1 to 3 or 4°C assumed a tense fetal posture (minimum exposure of surface) and shivered violently (Text-fig. 8). At the same time, the temperature on the surface of the almost-dry to dry body ranged from 7 to 30°C and similarly on the flippers from 22 to 37°C . Breathing and heart rates were the highest recorded at any temperature, and an elevated metabolic rate was also indicated by the intense shivering. Adults under similar conditions showed comparable skin temperatures but were clearly more comfortable and relaxed.

We have seen that adult walrus readily expose themselves to air temperatures as low as -20°C with light winds (Fay & Ray, 1968), and they are known to lie in the open occasionally in much colder weather (Freuchen, 1935).

The calves continued to shiver intermittently up to an ambient temperature of 7 or 8°C but

only occasionally at temperatures of 10°C or more. Their posture became more relaxed, and there was a significant decline in the breathing rate. Between 10 and 15°C , they became fully relaxed and lay on their back or sides with flippers limp and away from the body. Adults under comparable conditions behaved in the same way, and their skin temperatures, like the calves', were sustained at 25 to 32°C ; the flippers of the calves were sustained at 30 to 37°C , i.e., near or at the temperature of the body core.

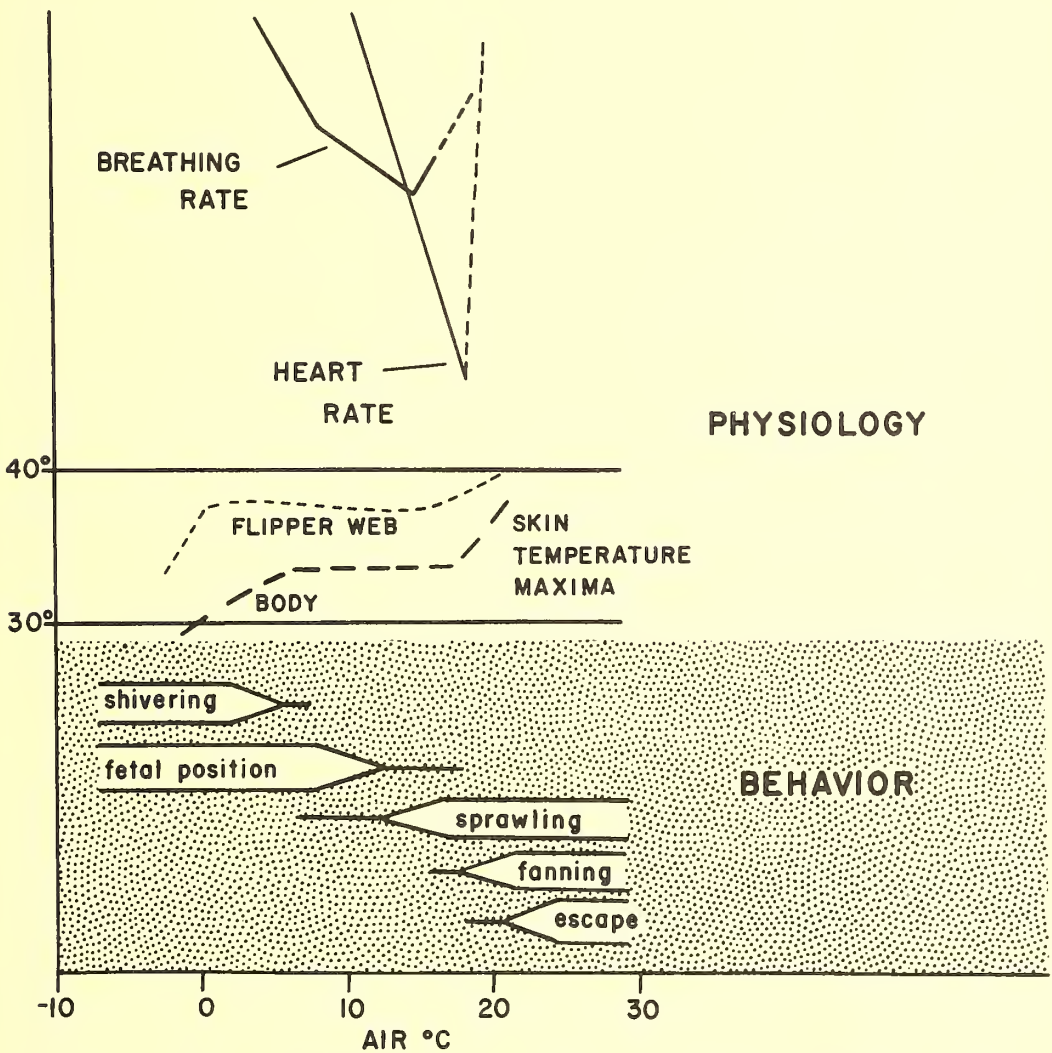
Breathing rates of the calves declined to the lowest recorded levels at an air temperature of about 15°C , and minimum heart rates occurred at 18 to 20°C . The calves, in general, became restless at the latter temperatures, sprawling for maximum exposure of surface and fanning with the fore flippers. At this point also, skin and flipper temperatures rose above the previously sustained levels, indicating a major increase in heat output and, we think, of heat production. Ultimately, when air temperatures reached more than 20°C the calves "escaped" into the water, where they sometimes resumed their sleep.

The behavioral reactions of adult walrus

under comparably warm conditions were virtually the same as those of the calves. Sprawling and fanning were observed when they lay out in air at 8.5°C with intense midday insolation and no wind (latitude 66°, mid-May), and at 14°C with afternoon sun and 2-mps breeze (latitude 58°, mid-June). Conditions warmer than the latter are uncommon in the walrus' range but common to the south of it, where insolation is more intense and air temperatures generally higher.

The captive juveniles, with a history of one to five years' exposure to the temperate climate of Coney Island, New York, responded behavior-

ally in a pattern comparable to the calves'. They did not haul out often in air cooler than 3 or 4°C or warmer than 25°C, and when they did emerge under these conditions, they stayed for only a short time, usually returning to the water before their skin dried off. However, under most conditions, their skin was cooler than that of the calves, and in no case did their skin or flipper temperatures rise above the usually sustained levels. We assume that these differences reflect physiological maturation and acclimatization to temperate climate, with more efficient conservation of heat in cold weather and better dissipation of heat when the weather was warm.



TEXT-FIG. 8. Correlation between characteristic physiological and behavioral responses of newly captured walrus calves and ambient still air temperatures in shade.

Limits of Thermoneutrality and Thermal Tolerance

Without actual measurements of metabolic rates, we could not determine the exact limits of thermoneutrality in either the calves or the adults, but the indirect evidence was strongly suggestive of some general parameters. From the calves' highly variable skin and flipper temperatures, high breathing and heart rates, and, especially, intensive shivering at still air temperatures of 5°C and lower, we estimate that the lower limit (= critical temperature) of their thermoneutral zone was probably about 5°C. Their shivering alone was indicative that metabolism was increased above the basal rate. For adults, the critical temperature is assumed to be much lower, but we do not know how low. Judging from their ostensible comfort at air temperatures near -20°C with light wind, we are confident that they can withstand at least that much cold without elevation of their metabolism.

We estimate that the upper limit of thermoneutrality for the nonacclimatized calves was at or near 18°C in still air and shade. This was based on analogy with other homeotherms, in which minimum breathing and heart rates occur usually at or near the upper limit of thermoneutrality (e.g., Bartholomew & Hudson, 1962; Hudson & Brush, 1962; Hudson, 1965), and elevated body temperatures are correlated with increased metabolism (e.g. Graham *et al.*, 1959; McNab & Morrison, 1963). Elevation of body temperature in the walrus calves was indicated by the rise of flipper temperature above 37°C at air temperatures over 18°C, for the flippers could not have become warmer than the normal body core unless the core temperature itself had risen. Also possibly indicative were the high rectal temperatures recorded occasionally from calves introduced to temperate climate.

The upper limit of thermoneutrality for adults is unknown but is believed to be similar to that of the calves. This is suggested principally by their comparative behavior (Fay & Ray, 1968). Adults at the southern edge of their geographic range in summer, in 14°C air with sunshine and light breeze, showed signs of heat stress (hyperemia, sprawling, restlessness, fanning) comparable to those in calves in still air and shade at 18°C or more. The added heat from the sun in that situation was equivalent to at least an additional 10°C of air temperature and was only partly counterbalanced by the breeze. From their behavior, we judged that the majority of these animals would not have tolerated much warmer weather. A high proportion of them had already withdrawn into the sea.

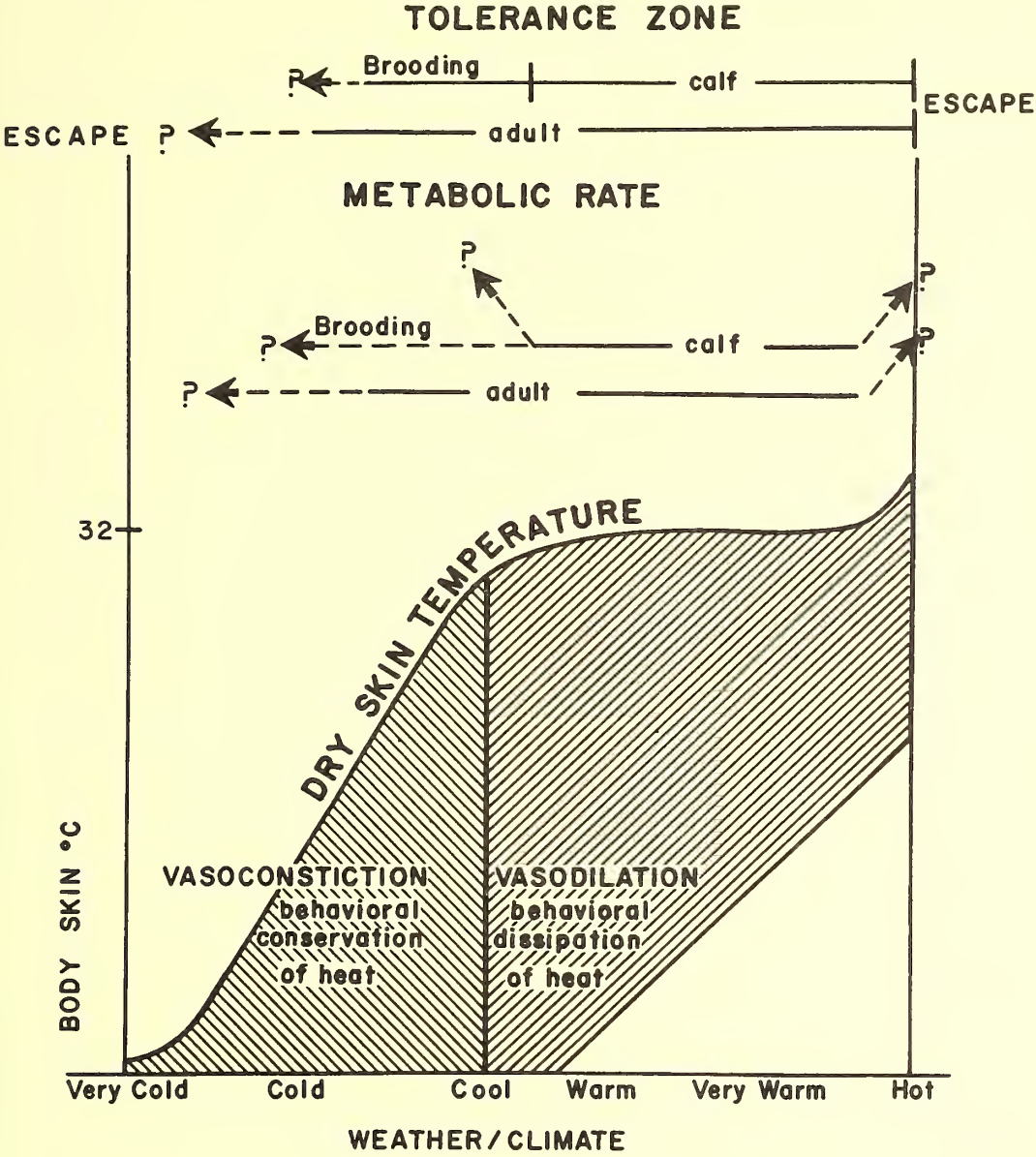
The general scheme, as we envision it, of wal-

rus' reactions to the thermal climate in air is shown in Text-fig. 9. Here, the scale of thermal conditions (abscissa) is necessarily vague because individual animals will be influenced not only by air temperature but by wind, solar radiation, moisture, and the conductivity of the substrate. These combine to present an "effective" temperature that could not be considered in detail here (cf. Ray & Smith, 1968).

Their reactions may also vary with individual and seasonal differences in acclimatization, the thickness of their insulation, their maternal status, the molt, and their general physical and nutritional condition. Molting animals seem to be more sensitive to cold and less sensitive to heat than any others; cows with newborn calves and sick or exhausted animals tend to be least sensitive to either. Tolerance will vary also with the number of animals in the group. Large herds can be expected to tolerate more intense cold than isolated animals because of their huddling and mutual improvement of the microclimate. Conversely, huddling groups will be less tolerant of heat because of their reduced surface area. Indeed, the gregariousness and persistent huddling of walrus may be among the most influential factors determining the limits of their thermal tolerance.

The limits of tolerance are shown as being somewhat wider than the estimated limits of thermoneutrality. This is based mainly on the reactions of the calves, in which escape evidently was not induced until the metabolism had risen above the basal level. In the captive juveniles and the adults, the two zones may have coincided exactly. We believe that wild walrus usually avoid exposure to conditions outside of their thermoneutral zone and that the principal function of the escape reaction is the withdrawal from unfavorable conditions. Whereas the attainment of thermoneutrality may often be feasible in air, it probably is always feasible in the water in healthy animals due to the normal condition of vasoconstriction.

The question of why walrus haul out at all, if they can sleep in the water with minimum production of heat, may be answered by considering the metabolic requirements of their skin. For conservation of body heat during immersion, the skin is permitted to cool to about the same temperature as the water and is largely deprived of blood due to vasoconstriction. The epidermis, which comprises the outermost layer, in direct contact with the medium, is most affected. At the low temperatures normally sustained during immersion, the epidermis is evidently in a semidormant state and is incapable of performing its growth and reparative func-



TEXT-FIG. 9. Schematic representation of dry skin temperature and its relation to the tolerance zone and metabolic rate of walruses at rest in air. The critical physiological limits are not known for the walrus, nor are the exact points of escape with response to extreme low temperature. Thermoneutrality is predicted within the entire tolerance zone and is considerably extended in calves by maternal brooding (Fay & Ray, 1968). Acclimatization has the effect of shifting these predicted responses.

tions (Feltz & Fay, 1967). The optimum temperature for epidermal growth seems to be near 30°C, which is attainable in the skin of polar pinnipeds only when exposed to the air. By means of behavioral regulation of their surface area and its exposure to the air, walruses are

capable of sustaining the required skin temperature under a wide variety of climatic conditions. This is reflected in the plateauing of the skin/ambient temperature curve in the upper half or more of the zone of thermoneutrality.

The highest dry skin temperature on the body

during thermoneutrality is about 32°C. When this temperature is exceeded, walrus become restless, begin fanning, and ultimately withdraw into the water. We have seen that this occurs, mostly in huddling walrus, even in the relatively cool climate at the southern edge of the walrus' range, and we believe that warmer climates would be intolerable for this reason alone. Provided that these animals would retain their usual pattern of diurnal rest and nocturnal activity, as well as their thigmotactic and heliophilic behavior, we are confident that they could not reside in comfort at lower latitudes in summer. Walrus exposed to temperate climates while in captivity successfully avoided hyperthermia during the warmest weather by hauling out only so long as they were cooled by evaporation, or by hauling out at night. (Fay & Ray, 1968). However, because of their diurnal feeding schedule in captivity, they were not as closely bound to the normal activity rhythm. Some ancestral walrus evidently lived in warmer climates than their modern descendants (Ray, 1960; Mitchell, 1961, 1962), and the morphology of at least one of these suggests that it led a more pelagic existence.

SUMMARY AND CONCLUSIONS

1. The influence of climate on the distribution of walrus was investigated by measuring some parameters of physiological thermoregulation in unrestrained animals at rest, under natural and controlled conditions at ambient temperatures from -1 to 25°C. Data were obtained on the temperatures of the body core, skin, and hind flippers and on the breathing and heart rates and temperature gradients. Some comparative data were obtained from young walrus that were reared in captivity in a temperate climate.

2. Internal temperatures of wild adults and calves were relatively labile, ranging from 34 to 39°C. Rectal temperatures of calves may have fluctuated in response to several factors, including teething, high air temperatures, and time of day. The mean rectal temperature of ten subadults and adults under natural conditions in -1 to 14°C air was 36.6°C.

3. Skin temperatures on the body during immersion were within 3°C of water temperature but rose rapidly to higher levels after emergence and drying. In general, the flippers warmed more rapidly than the skin of the body and attained somewhat higher temperatures.

4. The skin and flipper temperatures of calves in still air and shade did not rise continuously with increasing ambient temperature, but leveled off between air temperatures of 0 and 15°C and then rose again under warmer conditions. The upper limit of skin and flipper temperatures in the plateau were about 32 and 37°C, respectively.

5. The breathing rates of calves were highest at air temperatures near 0°C. They declined to a minimum at 15°C and rose again at 18°C. Brief periods of apnea were most common in air warmer than 10°C. The minimum heart rate occurred at 18°C.

6. Temperature gradients in the skin, blubber, and outer muscles were about five times longer than those in young harbor seals under comparable conditions. This difference was correlated with the greater thickness of the skin and blubber in the walrus. Gradient length is as much a function of the thickness of insulation as of the internal temperature-skin temperature difference. It is not a function of air temperature when the walrus is dry and is affected by other factors such as insolation.

7. The estimated lower limit of thermoneutrality (critical temperature) of the calves in still air and shade is about 5°C; in adults it is probably lower than -20°C. Adults are assumed to be thermoneutral when at rest in the water.

8. The estimated upper limit of the zone of thermoneutrality for isolated calves and adults is about 18°C in still air and shade or its equivalent under natural conditions. Animals in these or warmer conditions showed elevated skin, flipper, and body temperatures, as well as cutaneous hyperemia, restlessness, and fanning. Ultimately, they avoided further hyperthermia by withdrawing into the water.

9. The weather in spring and summer at the southern edge of the walrus' geographic range is often warm enough to induce hyperthermia and withdrawal to the water at a time when basking may be particularly important, especially during annual molt. Without physiological acclimatization and some major alterations of their more stable behavioral characteristics, such as diurnal inactivity, heliophilism, and huddling (which are adaptive for cold climates and not for warmth), walrus probably would not or could not occupy areas with warmer weather.

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Thermoregulation of the Pup and Adult Weddell Seal, *Leptonychotes weddelli* (Lesson), in Antarctica.

CARLETON RAY¹ AND M. S. R. SMITH²

(Plates I-II; Text-figures 1-8)

INTRODUCTION

SOME phocid seals are the most polar of marine mammals and live in the thermally most difficult of environments for homeotherms. They are confronted with extreme problems of heat conservation in the coldest of seas and with problems of heat dissipation when hauled out on the ice to pup, molt, or rest. Their thermoregulation, therefore, illustrates some important facets of mammalian adaptation.

The Weddell seal, *Leptonychotes weddelli* (Lesson), is typically an inhabitant of the shore and fast ice of Antarctica, frequenting the most southerly open water, leads, or access holes. It probably lives at the lowest mean environmental temperature of any mammal on a year-around basis. The water of its environment is almost always close to the freezing point even in summer, when air temperatures rarely rise above 5°C. Its biology has been reviewed by Wilson (1907), Lindsey (1937), Bertram (1940), Sapin-Jaloustre (1952), Scheffer (1958), Mansfield (1958), King (1964), and Smith (1965, 1966). Recently, attention has been turned to its underwater biology, for instance, Littlepage (1963), Ray and Lavallee (1964), Kooyman

(1965), Schevill and Watkins (1965), and Ray (1965, 1966, 1967). The species is an ideal subject for field study.

Previous work on the thermoregulation of pinnipeds, such as the important studies of Irving and Hart (1957) and Hart and Irving (1959), has for the most part emphasized physiological aspects in restrained animals: the skin/ambient temperature regression, the metabolic rates, the definition of thermoneutrality, and the establishment of critical temperature limits. Fay and Ray (1968) and Ray and Fay (1968) have used a somewhat different approach in which behavioral and physiological mechanisms were considered simultaneously in wild and unrestrained captive walruses. Their remarks and methods apply here: in sum, that wild animals rarely expose themselves for prolonged periods to conditions where critical limits apply; that a "tolerance zone" in which thermoneutrality is maintained is more applicable for animals in nature; that behavior (including "escape") and physiology are mutually responsible for the delimiting of this zone; and that a study of the unrestrained animal helps to reveal the relationship between physiology and behavior.

In the present study we report on work done almost solely on unrestrained Weddell seals in the field in Antarctica in an effort to delimit the tolerance zone of the Weddell seal. In addition, some years ago it was suggested to one of us (Ray) by L. Irving (pers. comm.) that one aspect of pinniped thermoregulation had been ignored: the physiological change that the

¹Department of Pathobiology, School of Hygiene and Public Health, The Johns Hopkins University, Baltimore, Maryland. Formerly, Curator, New York Aquarium, New York Zoological Society, Coney Island, New York.

²Department of Zoology, University of Southampton, United Kingdom. Formerly, Zoology Department, University of Canterbury, Christchurch, New Zealand.

lanugo-clad, almost blubberless, mostly terrestrial pup undergoes to become a more thinly haired, thick-blubbered, amphibious postlanugo animal. Since that time, the work of Davydov and Makarova (1964) has appeared, in which pup harp seals, *Phoca groenlandica*, were subjected to metabolic tests. It was shown that metabolism decreases directly with the accumulation of subcutaneous fat and increases the tolerance of lower water temperatures. In the present study, we have dealt with the Weddell seal principally in air and have utilized almost identical methods for pups, juveniles, and adults on the assumption that the changes in the insulative layers from birth to weaning are responsible for no less significant changes in behavioral and physiological thermoregulation. In contrast with Davydov and Makarova, we have not utilized an experimental approach, but rather an ecological one. As in Fay and Ray's work, we have paid particular attention to adaptations for heat dissipation near the upper tolerance limits, partly owing to difficulties of observation in cold or inclement weather.

MATERIAL AND METHODS

Data were gathered almost entirely from wild and penned animals in Antarctica. Wild animals were easily accessible by tracked vehicle from McMurdo Station. Penned animals were two adult females and their pups that were netted and airlifted by helicopter to wood-slatted, 5-by-5 meter pens placed on the sea ice 0.5 kilometer west of McMurdo Station.

During the spring season when most of our work was done, Weddell seals were mostly gathered in rookeries or smaller nonbreeding groups from Scott Base, Hut Point Peninsula, to Cape Royds: i.e., between 77° 33' and 77° 52' south latitude, and 165° 5' and 166° 53' east longitude. Temperatures are not so extreme as they are in the interior of the continent, but are more so than in similar arctic latitudes, owing to higher velocity winds of colder temperatures from the south polar plateau.

Physiological measurements were made on slightly disturbed or undisturbed animals except for thermal gradients in the superficial tissues of adults, which were taken immediately after death from animals killed for other purposes (dog food, specimens). A few observations were also made for comparative purposes on captives that were returned to the New York Aquarium, but no physiological data from them are indicated on our graphs. Skin samples were taken in the field and returned to New York for tanning and study. Respiratory and heart rates were

taken visually, or, in the case of the latter, occasionally by means of a Cambridge Trans-Scribe electrocardiograph. Temperatures were taken with a six-channel Yellow Springs telethermometer; the most efficient probe proved to be a 20-gauge hypodermic type, which stabilized rapidly. A few temperatures were taken with Weston thermocouples when the telethermometer was not available. Rectal temperatures were taken on 15- to 30-cm penetration unless otherwise specified.

One pup was kept crated for a time in front of the biological laboratory for metabolic tests. When the gut was empty, the pup was sealed for one to two hours in a sheet-steel chamber, 1-by-1-by-2-meters, from which air samples were taken from two heights with 10-cc syringes through rubber stoppers in the chamber. Gas analyses were made with a Scholander 0.5-cc analyzer (Scholander, 1947).

Orientation and behavior studies were made visually from the ground and from the air. Aerial photography was used most to determine orientation to the sun.

In an effort to standardize, we made extensive tests to determine the best location on the seal's body for the taking of skin temperatures. In all cases, unless otherwise specified, temperatures are those from the dry body or flipper perpendicular to the sun, or, if in cloudy weather, farthest from the ice surface. This minimized the effects of dampness and vasoconstriction. Data from wet animals were treated separately. In a few cases, we were able to take skin temperatures from submerged or recently emerged animals to note the extent of vasoconstriction upon exposure to ice water.

For every physiological measurement, micro-environmental weather data were taken. Being cognizant that ambient shade temperature is not the only parameter of weather that affects thermoregulation, we have used "effective temperature" (cf. Eagan, 1964, & Folk, 1966), calculated here as follows: the black-bulb temperature in still air was taken in the seal's micro-environment as a measurement of insolation, and from this temperature one degree centigrade for every mile per hour of wind was subtracted. There was a slightly better alignment of data when using effective rather than ambient temperatures (Text-figs. 1-4), but the major advantage was that effective temperature gives a more realistic environmental parameter when insolation and/or wind are strong. For instance, Fay and Ray (1968) have shown that insolation and wind act independently of ambient temperature in influencing behavioral thermoregulation.

The dotted lines drawn on the graphs of Text-figs. 1-4 are our estimates of maximal skin temperatures in air. It is neither practical nor realistic to use statistical methods (i.e., regressions) in this work since "plateau" limits of temperature during vasodilation (Ray & Fay, 1968), not "average" skin temperatures, are probably more meaningful in adaptation.

RESULTS

Internal Temperatures

Only five measurements were made rectally but indications are that the internal temperature of the Weddell seal is close to 37°C. Three rectal temperatures of penned pups were all 37°C. The importance of adequate penetration into the rectum is illustrated by other two temperatures taken in adults: 5°C circumanally and 28°C upon only 7.5-cm penetration. Both of these animals were lying on ice in subfreezing air. Thermal gradients (Text-fig. 7) also indicate a core temperature at or very near 37°C, as indicated by deep blubber and muscle measurements near this temperature.

Temperature of the Skin When Wet

We had few opportunities to obtain surface temperatures on swimming, wild Weddell seals (Table I). One slightly active adult in the water

tive temperatures as high as 11°C. The highest skin temperatures were obtained upon emergence into air of the warmest effective temperature, in agreement with data obtained for walruses by Ray and Fay (1968).

Temperature of the Dry Fur and Skin

For adults, temperatures of the outer fur surface and the skin were taken from the same location on the body. For pups, the same applies, but the 2.0-2.5-cm thickness of the lanugo made possible the additional measurement of fur temperatures 1 cm beneath the surface. For both adults and pups, the skin temperatures of the flippers were taken at the flipper tip and on the membrane halfway to the tip from the ankle.

Adult fur-surface temperatures were usually not more than about 10°C higher than effective temperatures until about freezing, when the gradient was greater (Text-fig. 1). Fur temperatures rose as a straight regression with effective temperatures. Skin temperatures were considerably higher than fur temperatures. None was below freezing, but some were as low as 0 to 7°C at effective temperatures of -13 to -21°C. Skin temperatures did not rise as a straight regression with effective temperatures, but reached a plateau of about 34°C at effective temperatures over -13°C.

Pup fur-surface temperatures were similarly

TABLE I
SKIN TEMPERATURES OF WEDDELL SEALS WHEN IN WATER OR JUST EMERGED

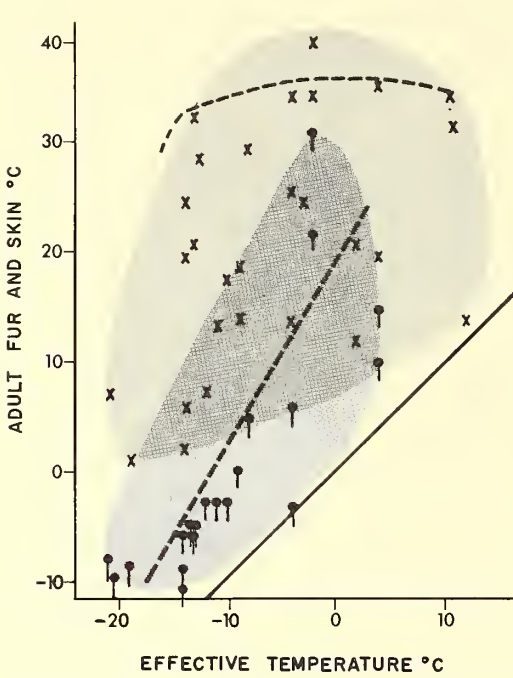
Effective Air Temperature	Water Temperature	Skin Temperature	Flipper Temperature	Remarks
-6.0	2.5	8.5	Adult, just emerged
....	-2.5	-2.0	Adult, in water
11.0	20.0	18.0	Adult, recently emerged
-19.0	10.0	2.0	Pup, just emerged
-19.0	-2.5	-1.0	Pup, just emerged
11.0	23.0	16.0	Pup, just emerged

of an access hole had a skin temperature a fraction higher than the supercooled -2.5°C water, confirming the data of Irving and Hart (1957). Just under the ice surface, the water temperature was -1.9°, in which case the water/skin gradient would be slightly smaller.

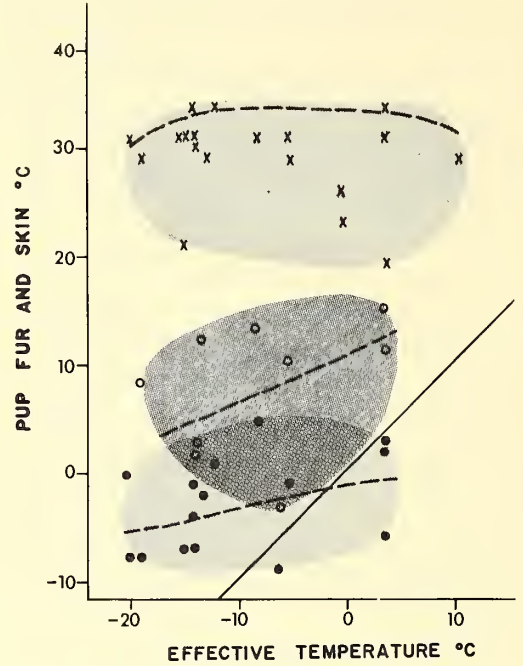
We were able to obtain data from five just-emerged animals (Table I). All animals tested had been out of water less than five minutes and most about a minute, yet skin temperatures rose in that short time to a maximum of 23°C and flipper temperatures to 18°C in air of effec-

low at low effective temperatures but did not rise as fast as those of adults (Text-fig. 2). We attribute the presence of fur-surface temperatures lower than the effective temperatures (in the upper range) to the fact that their fur was often slightly damp from melted snow. The fur temperature a centimeter below the fur surface was considerably higher than the fur-surface temperature. Skin temperatures were almost always high, plateauing at about 34°C at effective temperatures from -20 to 10°C.

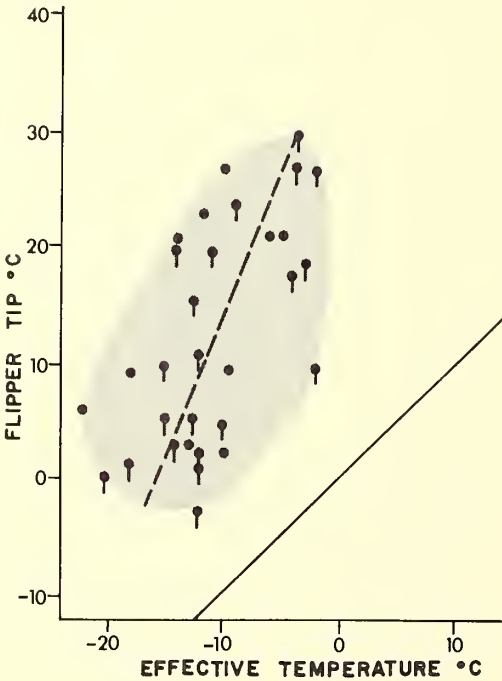
The flipper tip temperature of adults and pups



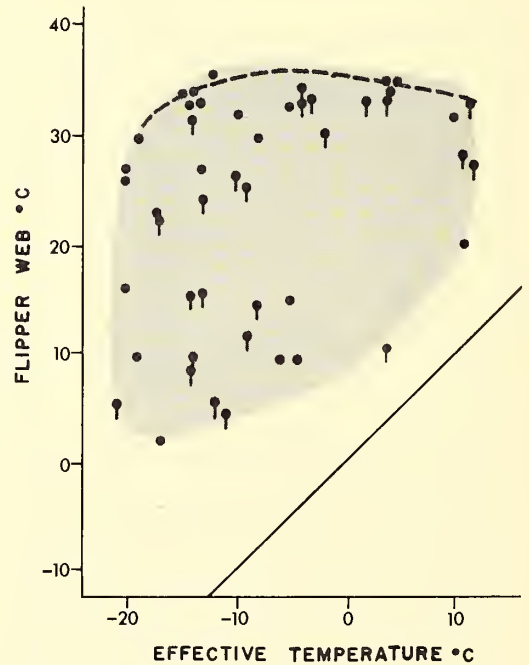
TEXT-FIG. 1. Temperatures of the dry fur surface (= ▼) and skin (= x) of adult Weddell seals at rest in air.



TEXT-FIG. 2. Temperatures of the fur surface (= ●), fur 1 cm beneath the surface (= ○) and dry skin (= x) of pup Weddell seals at rest in air.



TEXT-FIG. 3. Temperatures of the flipper tip of adult (= ▼) and pup (= ●) Weddell seals at rest in air. The flipper tip was often wet or damp.



TEXT-FIG. 4. Temperatures of the dry flipper web of adult (= ▼) and pup (= ●) Weddell seals at rest in air.

rose as straight regressions with effective temperature (Text-fig. 3). The temperature at the tip of the flipper descended to -4°C at an effective temperature of -13°C and rose to 30°C at an effective temperature near freezing. The flipper tip of both adults and pups was often damp with melted snow, urine, or excrement. The flipper membrane of adults and pups was similar to the body skin temperature, reaching plateaus of about 34°C at effective temperatures over -15°C (Text-fig. 4).

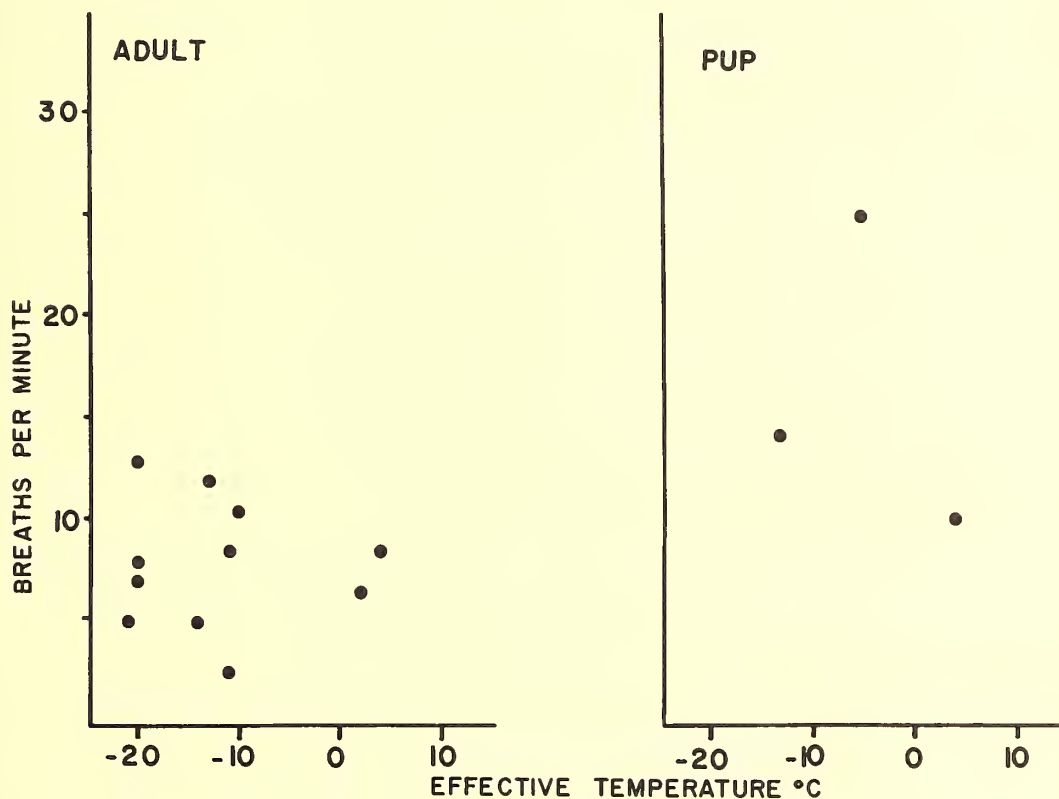
Data were also obtained for skin temperatures from the base of the flipper (ankle) and the pelvic region (hip) in an effort to establish a gradient from flipper tip to body. However, these results were indistinguishable from each other and from temperatures of the body skin and flipper web and so are not figured.

Vasoconstriction for body skin, where temperatures would not rise to plateau levels, might occur at effective temperatures below about -13°C for adults and -15°C or lower for pups. Our estimated slopes, shown by dotted lines on Text-figs. 1-4, indicate that skin temperatures

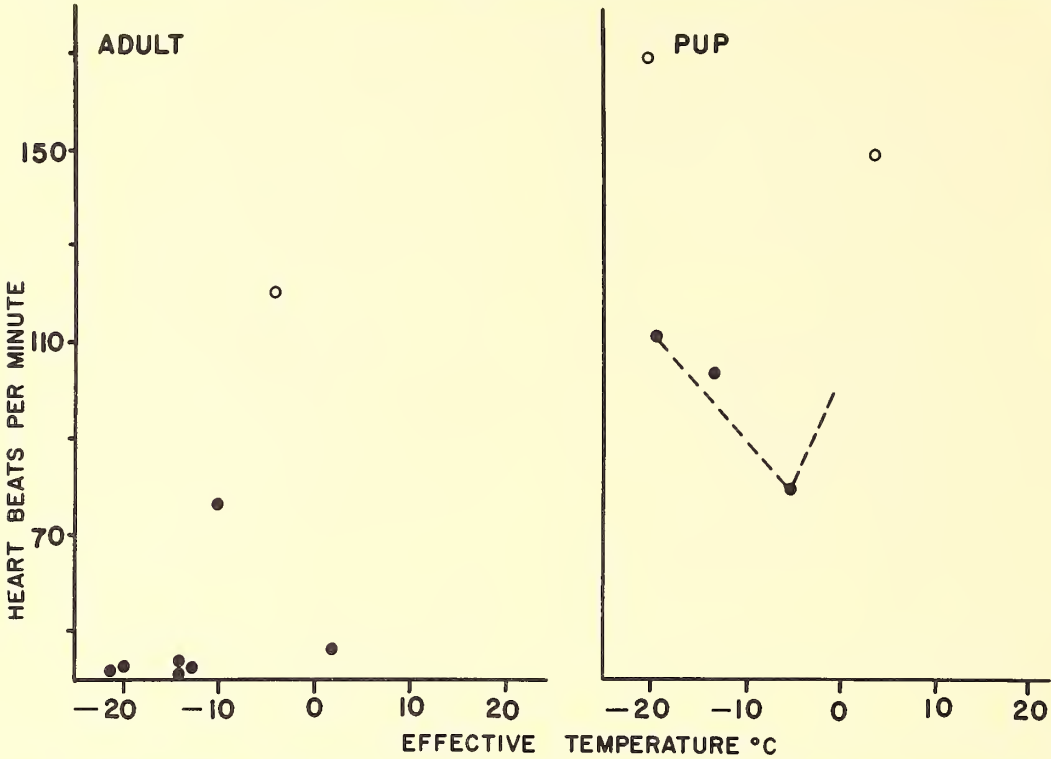
might not descend to 0°C until effective temperatures of at least -30°C are attained, but data at these low effective temperature levels are not available.

Breathing and Heart Rates

Our few data, all from resting animals, are presented in Text-figures 5 and 6. It is immediately apparent that pups had higher breathing and heart rates than adults, reflecting higher metabolic rates as well. For adults, the average heart rate was 56 per minute and the average breathing rate was 7.8 per minute. For pups, these rates were 123 and 16.3, respectively. It was noted that marked bradycardia occurred when the breath was held and that both rates were highly irregular. Heart rates taken by aid of an electrocardiograph were relatively high owing to the disturbance caused to the animal. We were unable to demonstrate a correlation of these rates with effective temperature, as for walruses in Ray and Fay (1968), though it is possible that pup heart rates were minimal at about -5°C effective temperature.



TEXT-FIG. 5. Breathing rates of adult and pup Weddell seals at rest in air.



TEXT-FIG. 6. Heart rates of adult and pup Weddell seals at rest in air. ○ = rates taken by electrocardiograph.

Metabolic Rates

Seven tests of from 15 minutes to one hour duration on a pup Weddell seal showed rather consistent results (Table II). Oxygen consumption averaged 35.3 cc/min/k^{3/4} and carbon dioxide production was 25.5 cc/min/k^{3/4}. The respiratory quotient (R.Q.) was 0.727. High metabolic rates for seals have previously been shown by Scholander (1940), Scholander, *et al.* (1950), Irving and Hart (1957) and Davydov and Makarova (1964). Very few mammals show such exception to the Benedict "mouse to

elephant curve" (Brody, 1945, p. 370; Kleiber, 1961, p. 201). Though we do not compare our tests with those of others, because a pup was used and some elevation of rate is to be expected, we do wish to note the extremely high metabolic rate found here.

Thermal Gradients in the Superficial Tissues

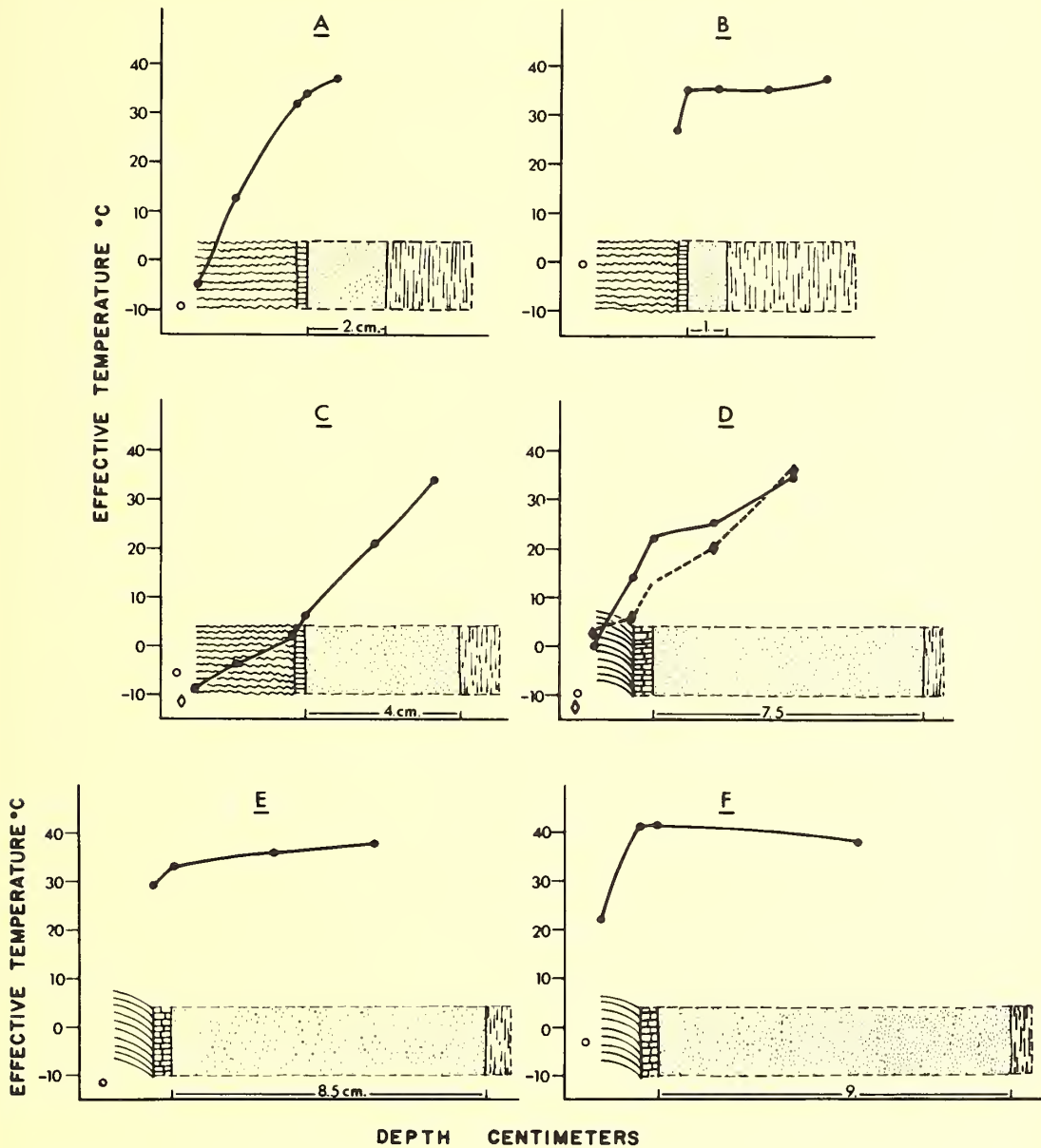
Temperature gradients were recorded through the fur, skin, and subcutaneous tissues of living pups and of adults immediately after they were killed (Text-fig. 7). In young pups without much

TABLE II
METABOLIC RATES OF A PUP WEDDELL SEAL

Chamber Temperature	O ₂ cc/min/k ^{3/4}	CO ₂ cc/min/k ^{3/4}	R.Q. CO ₂ /O ₂	Duration of Test, Minutes
3 to 6	40.9	28.7	0.702	15
5 to 8	16.9	12.5	0.740	15
-3 to 0	26.5	18.8	0.709	15
-2 to 4	43.8	30.7	0.706	60
0 to 1	42.25	30.75	0.727	30
-1 to 3	39.8	30.5	0.766	30
-1 to 3	36.5	27.0	0.740	15
Averages	35.3	25.5	0.727	

blubber (7A & B), skin surfaces were 32 and 27°C at effective temperatures of -8 and 0°C. Gradients were taken up mostly in the thick lanugo coat. In contrast, a fat pup (7C), well toward weaning and damp at the time of recording, had a low skin temperature, illustrating the

effect of dampness in inducing vasoconstriction. Three examples of adults illustrate three contrasting gradients. The first (7D) contrasts temperatures from the shaded side with that of the sunny side of the seal. The gradient was not so steep in shade as under direct insolation. Con-



TEXT-FIG. 7. Temperature gradients through the superficial tissues of pup and adult Weddell seals immediately after death. Skin and blubber thicknesses at the site of measurement are indicated beneath each section. Air temperatures within 1 meter of the animal are indicated by the open circle to the left of each section. Lanugo = wavy lines. Adult hair = curved lines. Skin = horizontal lines. Blubber = stippled area. Muscle = vertical lines. On section D, diamonds connected by a dotted line indicate a gradient through the tissues on the shaded side of the seal.

trasting was an example of elevation of skin temperature to plateau levels (7E) in which the gradient is mostly in the fur. The last (7F) shows the effect of intense insolation in which the skin was over 40°C and deeper tissues 38°C, indicating that heat gained at the surface was distributed to other parts of the body through the circulatory system. Ray and Fay (1968) show a similar situation in the walrus in which high surface temperatures are induced by insolation.

Effect of Insolation on Fur and Skin

The lanugo of the Weddell seal is silver-tan to gray in color, darkest on the back (Plate I). Flat wavy hairs form a thick coat about 2.0-2.5 cm thick. Short hairs of the juvenile coat are present under the lanugo from birth and grow to replace the lanugo at about four to six weeks of age. The juvenile and adult coats are medium to dark gray, darkest on the back, flecked with black and white irregular blotches and spots, especially below. The primary hairs are flattened and about 1 cm in length, pointing backward, but tending to curve forward when dry. There are fine secondary hairs about 0.5 cm in length. Scheffer (1964) gives the density of primary hairs, on formalin-preserved skin, as 34/cm² with a maximum length of 1.3 cm, and the number of secondary hairs per unit as three to five.

Five tests were made of the effect of insolation on tanned skins of pup and adult seals. Skins were spread half in shade and half under strong sun. Ambient shade and black-bulb temperatures under sun were taken adjacent to the skins. The results of the tests were almost identical and examples of adult and pup will be considered (Text-fig. 8 A & B). Air temperature in shade did not change throughout the tests. Skin and fur-surface temperatures in shade rose somewhat higher than air temperatures in shade for both adult and pup, probably owing to radiation reflected from a nearby white building. Black-bulb temperatures in sun rose rapidly, but fur-surface and skin temperatures of adult and pup rose faster and to a higher level. Cloudiness occurred about two-thirds through the tests and produced a fall in black-bulb temperatures with a corresponding fall in skin and fur temperatures.

Several explanations are possible for the rapid and extensive rise in skin and fur temperature under sun. The simplest is analogous to that of Krog (1955) for pussy willow catkins. The shiny, translucent hairs allow sunlight through to the skin, where heat is absorbed, but they do not allow as much heat radiation to escape. The result is the familiar "green house" effect.

A second phenomenon, a lenticular effect of the flattened hairs in concentrating the sun's rad-

iation, may also be in evidence as suggested by Fay (pers. comm.). Adult hairs are flatter and more regularly arranged than pup lanugo, and we see that adult skin temperature rises faster and higher than that of the pup. However, in the increasing cloudiness indicated, the adult skin temperature fell, whereas the thick lanugo trapped warm air so that no similar fall in the pup skin temperature was observed.

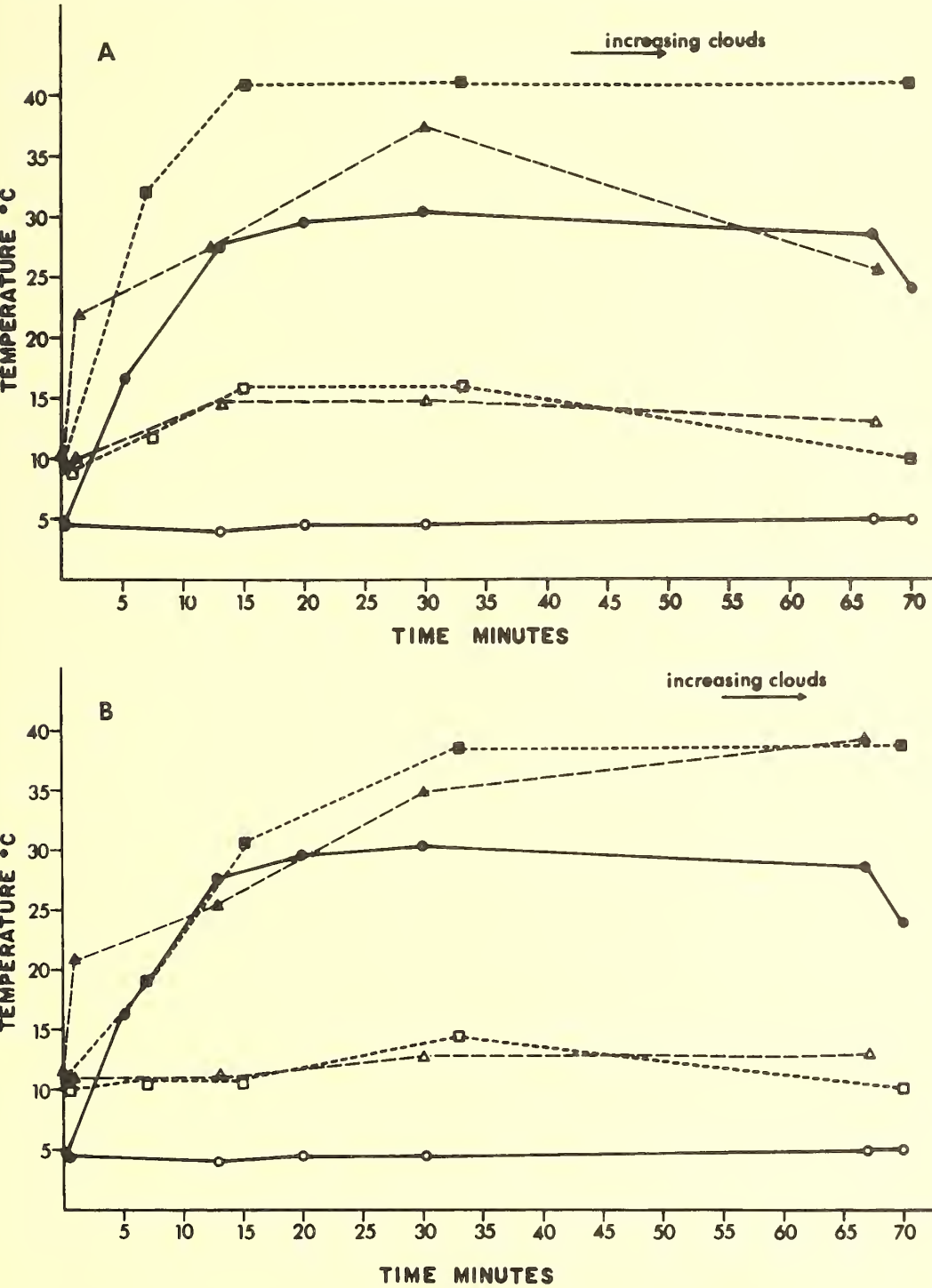
The Role of Behavior

The Weddell seal does not exhibit the array of thermoregulatory behavior displayed by walruses (Fay & Ray, 1968). Nevertheless, some behavioral patterns are marked. The most notable of these is the predilection of the Weddell seal for sun. On hot, dry days Weddell seals were observed basking on the surface in numbers not seen in the same localities during inclement weather. During sunny weather, the seals, especially pups, moved about on the ice; it appeared to us that flippers were spread more than during cloudy weather and that the seals sought the sun's ray by orienting with their long axis perpendicularly to them. To test the latter point, seals were counted, principally from the air, and their orientation to the sun recorded photographically (Table III). During cloudy weather about half the seals were oriented perpendicularly to the sun, but during sunny weather about four-fifths were oriented in this way. Plate II shows two examples of aerial photographs from which data were taken.

During inclement or very cold weather, Weddell seals are notably either sluggish in air or retreat to water (Smith, 1965). However, escape to water is usually not possible for mothers and their pups. At these times, pups remain in the lee of their mothers, moving out of the lee and resuming activity only when effective temperatures reach about -20°C. We have some evidence that mothers induce activity on the part of the pups and/or that nursing keeps the pups somewhat active even in the harshest weather. This probably serves to prevent drifting in and allows crystals of frozen moisture to fall off, thus keeping the lanugo fluffy and dry. Plate I shows a pup and its mother just after a severe blizzard. The pup has resumed activity and is thus dry and warm and free of snow.

DISCUSSION

Scholander (1955), in reviewing the climatic adaptations of homeotherms, has reasoned that clues to thermoregulation are principally to be found in the control of heat dissipation. He has further stated that basal metabolic rate and internal temperature are not adapted to climate and that physical insulation and adaptation of



TEXT-FIG. 8. The effect of insolation on the fur and skin surfaces of tanned, dry adult (A) and pup (B) Weddell seal skins. Air temperature in shade (—○—). Black bulb temperature in sun (—●—). Fur surface temperature in shade (—△—). Fur surface in sun (—▲—). Skin surface in shade (—□—). Skin surface in sun (—■—).

TABLE III
ORIENTATION OF WEDDELL SEALS TO SUN

Sky	Total Seals	Percentage of Total Perpendicular to Sun
Clear-sunny	63	65
	28	78
	40	70
	68	76
	33	79
	16	71
	32	66
	60	92
	4	100
	13	77
	24	100
	16	88
	19	79
	14	86
	12	92
	28	64
	28	68
	24	79
	64	83
	40	63
	41	73
	26	85
	62	84
	31	81
	44	89
	Average percentage 79.5	
Cloudy or partly cloudy	38	50
	100	60
	64	70
	68	53
	40	45
	33	58
	46	39
	34	56
	82	49
	76	47
	49	53
	35	51
	41	56
	90	52
	Average percentage 52.8	

critical temperatures are the major mechanisms for heat dissipation control. These observations strongly imply that skin temperature should vary directly with ambient temperature in order exactly to balance metabolic heat production with heat dissipation. Irving and Hart (1957) and Hart and Irving (1959) show such regressions for restrained seals in experimental conditions.

Fay and Ray (1968) and Ray and Fay (1968) have found that for wild and unrestrained walrus, a plateau of skin temperatures rather than a straight regression is the case and

that behavior is at least as important as physical or physiological mechanisms in thermoregulation. Further, tolerance limits, rather than critical physiological limits, were indicated to be significant in an animal that, by behavioral means, is probably able to maintain thermoneutrality beyond the limits indicated by physiology alone. The present study on the Weddell seal confirms the observations made for the walrus. Our results indicate, following the suggestion of Brody (1945, p. 295), that although critical values are theoretically interesting, they probably have little significance under natural conditions.

The Weddell seal is a very large species, probably the heaviest except the elephant seal, *Mirounga sp.*, and the longest except the elephant seal and the leopard seal, *Hydrurga leptonyx*. The lanugo of pups is thick, as described above. The blubber appears to be the thickest of any seal except the elephant seal. At birth the nose-tail length is about 125 cm and the belly blubber measures about 1 cm. The blubber is about 5 to 6 cm at weaning, when the pup has grown to about 160 cm. Yearlings are 160 to 180 cm long and have about 4 cm of blubber in November. Females are inclined to be a little longer than males. Large ones are about 300 cm, and the blubber is 6 to 9 cm thick. Blubber is not of constant thickness the year around but varies with nutrition, nursing, and molting. Hart and Fisher (1964) have given thickness of blubber for several species, and the thickest given is that of the Arctic harp seal, at 6.3 cm. Since the tropical Hawaiian monk seal's blubber is 4.5 cm, the thickness of blubber is probably of little significance under conditions of vasodilation when blubber is bypassed by blood flowing to the surface. But blubber thickness is of significance under conditions of vasoconstriction. Therefore, a thick blubber becomes vitally important to polar species only when such a species is swimming in ice water or exposed to harsh conditions in air.

We have presented data that clearly show that the wild, unrestrained Weddell seal, like the walrus (Ray & Fay, 1968), vasodilates in air and that the dry skin temperature reaches a high "plateau" level of about 34°C. This high plateau is reached, however, only on that part of the seal not in contact with the snow or ice substrate, against which the skin is vasoconstricted. Heat gained on one surface of the seal is probably distributed through the body by the circulatory system. We have also shown that the Weddell seal actively seeks the warmth of insolation by orienting with the long axis of the body perpendicularly to the sun's rays.

As shown by the time-temperature curves of Text-fig. 8, Weddell seals are aided in the gaining of heat by what is familiarly termed the "greenhouse effect," wherein heat gained by the sun's radiation is conserved by an overlying layer of hair. This is a new observation for pinnipeds. It is primarily an adaptation in which Weddell seals are able facultatively to take advantage of insolation, when the latter is sufficiently strong, in an environment that is the coldest known for mammals. The saving of metabolic heat due to this efficient utilization of insolation is presumably considerable.

Pups in lanugo appear to be better adapted to temperatures well below freezing than to temperatures close to or above 0°C. Wet hair has little insulating value. At low temperatures, dampness from birth, melting ice, urine, or excrement freezes and falls off so that the lanugo remains fluffy and dry. Observations of late-born Weddell seals exposed to high temperatures and dampness tend to confirm this observation. For example, a seal estimated at about a week's age and still quite thin was observed during a warm, wet snow fall on November 7. After a few similar warm, wet days, this seal was found near its mother, still thin. After nine days it died. We speculate that the cause of death was chill accompanying dampness and near 0°C weather of the period. We have subsequently observed that early born pups gain weight faster than pups in warmer, wetter conditions. The function of the lanugo is to retain body heat and to prevent undue heat loss from skin, which must remain at relatively high plateau temperatures to grow (Feltz & Fay, 1967), and this is most effectively performed when the lanugo is dry and an effective insulator, even in very cold weather.

Insights into the critical limits of the Weddell seal were obtained while transporting them from Antarctica to the New York Aquarium and also during their gradual acclimatization to temperate climate there. In November 1963, six Weddell seals were flown from Antarctica to New York in about two days. Temperatures in the aircraft ranged from 12 to 28°C, the latter during a stopover in American Samoa, where air-conditioning facilities were limited. There, after an hour at 24 to 28°C, an adult male and female became hyperactive, even showing signs of delirium, tossing and rolling in their crates. Flipper temperatures were as high as 39°C and body skin as high as 37°C. Their breathing rates were 16 per minute, higher than any rates taken in the field. Both animals died within 12 hours of this exposure. Two pups showed similar stress, one biting its flippers and the other showing

greatly increased activity when air temperatures reached only 18°C. One of the pups also died shortly after leaving Samoa. Two remaining seals, a juvenile male and an adult female, remained calm and lived. The juvenile male astonished us by copiously taking water from a paper cup held for it. Thus, the upper critical temperature limit, suddenly imposed on Antarctic-acclimatized animals, is probably not reached at temperatures under 20°C.

The above mentioned female, juvenile, and pup and two additional Weddell seals brought from Antarctica in February 1965 underwent gradual acclimatization during the New York winter and spring. None of these showed ill effects from effective temperatures as high as 32 to 34°C, often lying out and basking, their skins fully dry, under the heat of the summer sun. They did not even choose to escape to the 12°C water constantly available to them. Similar acclimatization is indicated for walrus by Ray and Fay (1968), but the Weddell seal apparently acclimatizes to even higher temperatures than the walrus, as indicated by the lack of escape behavior. It is, therefore, probable that upper critical limits of acclimation and acclimatization (see Hart, 1957, for further definition) are not realistic parameters to be used for the Weddell seal in its natural environment.

We could not observe seals at their probable lower critical temperatures in the field and had no means to expose Weddell seals to extremely low temperatures in captivity. Wild seals were observed to escape from severe weather conditions lower than effective temperatures of -30°C by entering the water, and the number of seals on the surface appears to be directly proportional to effective temperature (Smith, 1965, 1966). However, judging from experimental work on the harp seal, *Phoca groenlandica*, (Irving & Hart, 1957), we would not expect the lower critical temperature to be above -40°C. A similarly low critical temperature is indicated here by virtue of the high skin temperatures found at effective temperatures of -20°C and below.

Thus thermoregulation of polar amphibious mammals, as pinnipeds, presents two different situations: that in air, where we believe vasodilation and high skin temperatures are normal, and that in water, where vasoconstriction and low skin temperatures are normal. In both, we think the animal seeks to maintain thermoneutrality. By behavioral means such as orientation to sun in good weather or escape to water or retreat to the lee of the wind in inclement weather, the Weddell seal, as the walrus, seeks to avoid critical limits and to delimit its tolerance zone. The

upper and lower in-air critical limits are not realistic parameters for assessment of natural adaptation but only indicate one of the many imposed limits that may be superseded by behavior, as in the case of walrus brooding (Ray & Fay, 1968). We conclude that upper critical temperatures are rarely if ever reached in the natural environment of polar pinnipeds. Lower critical temperatures are limited indications of adaptation because both the walrus and the Weddell seal rarely expose themselves to such low temperatures but choose to escape to water and maintain thermoneutrality there well before lower limiting in-air temperatures are reached.

The primary differences between the walrus and the Weddell seal appear to be found in the tolerance zone, its relationship to distribution of the species, and the behavior exhibited within it. The walrus, especially the calf, is much more sensitive to cold than the pup or adult Weddell seal. Both species show some escape to water in inclement weather of -20 to -30°C effective temperature, but the walrus probably does so nearer its lower critical limit than the Weddell seal. The lower critical temperature for walrus calves is about 5°C and the lower limit of tolerance is extended by brooding to a lower temperature. The Weddell pup tolerates at least -30°C . However, we wish to point out that much more work is needed on unrestrained pinnipeds at their lower tolerance limit. Data are better for higher temperatures, and the walrus probably is limited in its distribution by its upper tolerance temperature of about 18°C and the habit of persistent huddling. The Weddell seal cannot be so limited. It is able to withstand, and shows no escape from, climate not remotely possible in the Antarctic environment. In both, acclimatization is possible, but, again, in the Weddell seal to a higher temperature. Finally, the walrus exhibits an array of behavior that serves to extend the tolerance zone near to or beyond probable critical physiological limits whereas in the Weddell seal few traits of behavioral thermoregulation are shown. This difference might to an extent be due to the presence of a coat of insulating hair in the pup and adult Weddell seal, contrasted with the practically bare-skinned walrus.

SUMMARY AND CONCLUSIONS

1. Parameters of physiological function and behavior were measured in unrestrained Weddell seals in an effort to delimit the tolerance zone and its possible relationship to distribution. Surface temperatures were obtained on the fur, body skin, and rear flippers. Heart, breathing, and metabolic rates were obtained. Tanned skins

were placed under shade and in sun in order to measure fur- and skin-temperature changes with time. Our measure of ambient temperature is "effective temperature," which includes the effects of wind and insolation.

2. Few measurements were made of rectal temperature, but about 37°C appears to be normal.

3. Skin temperatures during immersion appear to be only slightly higher than water temperature. After the seals' emersion into air, skin temperatures rise rapidly, faster in warmer air.

4. Dry skin and flipper temperatures did not rise as straight regressions with air temperature, but leveled off at about 34°C at effective temperatures above -13 to -15°C for adults and pups. Pups had skin temperatures in excess of 30°C at effective temperature of over -21°C . Fur surface temperatures, however, did rise directly with effective temperatures.

5. There was little or no correlation between effective temperature and breathing and heart rates of adults or pups, except possibly for the heart rate of the pup, which may have been minimal at about -5° . Pups had extremely high metabolic rates, in excess of any seal yet tested.

6. Gradients through the skin and blubber show that most of the gradient is taken up in the lanugo of the dry pup and in the fur, skin, and blubber of the adult or wet pup. The blubber of the adult Weddell seal is thicker than that of any other phocid except the elephant seal.

7. Tanned skins under sun show a marked "greenhouse effect" in which both fur and skin temperatures rise faster and higher than black-bulb temperatures. A possible lenticular effect of the flattened translucent hairs of the adult is indicated in which the adult skin is warmed faster than that of the pup, but also cools faster in shade.

8. Behavioral thermoregulation is not as marked in the Weddell seal as in the walrus. Seals show orientation to sun and seek lee from winds and storms. They also show escape to water from harsh weather conditions.

9. The upper critical limit of the nonclimatized Weddell seal in air is in excess of 20°C and the lower limit in air is probably at least as low as -40°C . The upper limit is not a realistic parameter of in-air adaptation or of distribution. The lower limit is probably at least -40°C and is not often experienced by most seals because before that limit is reached they probably escape to water. The seal, like the walrus, probably maintains thermoneutrality when at rest in either air or water.

10. The principal difference between the pup and the adult Weddell seal lies in the lanugo hair of the latter. Its function has been found, as expected, to provide an insulative coat in which the thermal gradient may be taken up before sufficient blubber is present for that purpose. The lanugo is most effective when thoroughly dry and so the pup Weddell seal is best protected at low effective temperatures when moisture will freeze and not wet fur or skin.

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EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. Female and nursing pup Weddell seals, illustrating the color pattern and the texture of the fur.
- FIG. 2. Penned female and pup Weddell seals just after a severe storm. The female is still covered with snow and has not yet resumed full activity. The pup has resumed

activity with the result that the snow has fallen off, leaving the lanugo fluffy and dry.

PLATE II

- FIG. 3. Weddell seals at random orientation on a cloudy day.
- FIG. 4. Weddell seals oriented perpendicularly to the sun on a clear, sunny day.



FIG. 1



FIG. 2

THERMOREGULATION OF THE PUP AND ADULT WEDDELL SEAL, *LEPTONYCHOTES WEDDELLI* (LESSON), IN ANTARCTICA.



FIG. 3

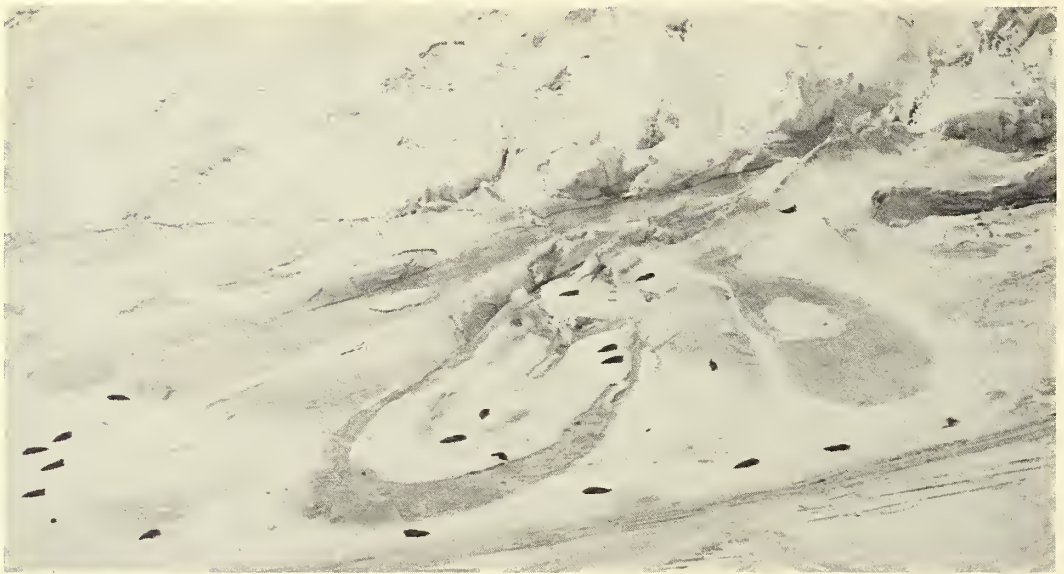


FIG. 4

THERMOREGULATION OF THE PUP AND ADULT WEDDELL SEAL, *LEPTONYCHOTES WEDDELLI* (LESSON), IN ANTARCTICA.

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The Pentastomes, *Waddycephalus teretiusculus* (Baird, 1862) Sambon, 1922 and *Parasambonia bridgesi* n. gen., n. sp., from the Lungs of the Australian Snake, *Pseudechis porphyriacus*¹

HORACE W. STUNKARD² AND CHARLES P. GANDAL³

(Text-figures 1-6)

INTRODUCTION

A FULL-GROWN SPECIMEN of *Pseudechis porphyriacus*, taken in Australia and purchased from a dealer, was received at the New York Zoological Park December 10, 1965, and died January 14, 1966. During this period it ate eight mice.

At autopsy, four large and 26 small pentastomes, all gravid females, were removed from the lungs. The pentastomes were killed and preserved in formalin. The large specimens, 45 to 50 mm. long, agreed in all particulars with descriptions of *Waddycephalus teretiusculus*, a species described originally by Baird (1862) as *Pentastomum teretiusculum* from the mouth of an Australian "copper-head" snake, *Hoplocephalus superbus* [*Denisonia superba*], which died in the gardens of the Zoological Society of London. A detailed anatomical study of the species was published by Spencer (1892) from material found in *Denisonia superba* taken on King Island, situated midway between the mainland of Victoria and Tasmania, and additional specimens that had been collected from the lungs of *P. porphyriacus* taken in Victoria. According to Spencer, the parasites were always firmly attached by their hooks with the heads buried deeply in the wall of the lung. A considerable pull was required to dislodge the creatures and

definite cavities were left. Spencer suggested that the specimen found by Baird in the mouth of the snake had migrated from the lung after the death of the host. Heymons (1935) stated that *W. teretiusculus* is widely distributed in Australia, and in addition to *D. superba* and *P. porphyriacus*, the parasite had been reported from the lungs of other Australian snakes: *Notechis scutatus*, *Demansia textilis*, and *Demansia psammophis*. Heymons (1941b) added that *W. teretiusculus* not only is common in Australian snakes but is parasitic in *Elaphe radiata*, a widely dispersed species that occurs in southern China, Bengal, the Malayan peninsula, Sumatra, and Java.

NEW MATERIAL

The present specimens are clearly members of the family Sambonidae Heymons, 1941, which comprises three genera: *Sambonia* Noc and Giglioli, 1922; *Waddycephalus* Sambon, 1922; and *Elenia* Heymons, 1932. The four larger individuals may be assigned positively to *Waddycephalus teretiusculus* (Baird, 1862). Indeed, Heymons' (1935, Fig. 1) drawing of the species might represent one of our specimens. These specimens are deposited in the American Museum of Natural History, No. 12927. The smaller individuals cannot be included in any of the described genera, and a new genus, *Parasambonia*, is erected to receive the new species that they represent. They are named *Parasambonia bridgesi*, in honor of William Bridges, for many years curator of publications and editor of *Zoologica*.

¹Investigation supported by Grant NSF GB 3606, continuation of G 23561.

²Research Associate, the American Museum of Natural History, New York, New York 10024.

³Veterinarian, the New York Zoological Park, Bronx, New York 10460.

Parasambonia n. gen.: Based on female only. Sambonidae; cephalothorax as wide as the abdomen; includes one or two cephalic annuli; sides of abdomen almost parallel; hooks simple, equal, median hooks slightly anterior to laterals; annulation often indistinct; lateral lines not apparent; about sixty annuli; uterine pore in sixth annulus from posterior end. Type species: *Parasambonia bridgesi* n. sp.

Differential diagnosis: *Sambonia* and *Elenia* are very similar; they are parasites of varanid lizards; the cephalothorax is small, much narrower than the abdomen, which is wide anteriorly and narrows to a stalklike posterior region; the hooks are very small, have a trapezoid arrangement with the anterior hooks somewhat larger than the posterior-lateral pair; lateral lines are recognizable. *Waddycephalus* is a parasite of Australian snakes, but it differs from *Parasambonia* in body form, gradually tapering posteriorly; the annulation is definite throughout with weak lateral lines; the hooks are unequal, the lateral pair smaller and anterior to the median ones. The most noteworthy difference between *Waddycephalus* and *Parasambonia* is the presence in the former genus of large glands, designated hook-glands by Spencer (1892), that extend along both sides of the intestine throughout most of the body.

Specific description, Parasambonia bridgesi n. sp.: The individuals of the smaller species were transferred to alcohol; twelve were stained in paracarmine or haematoxylin and mounted whole (Text-fig. 1); two were cut in transverse serial sections and stained with haematoxylin and erythrosin. The specimens are very uniform in size; they are slightly flattened ventrally and convex dorsally. They vary from 25 to 30 mm. in

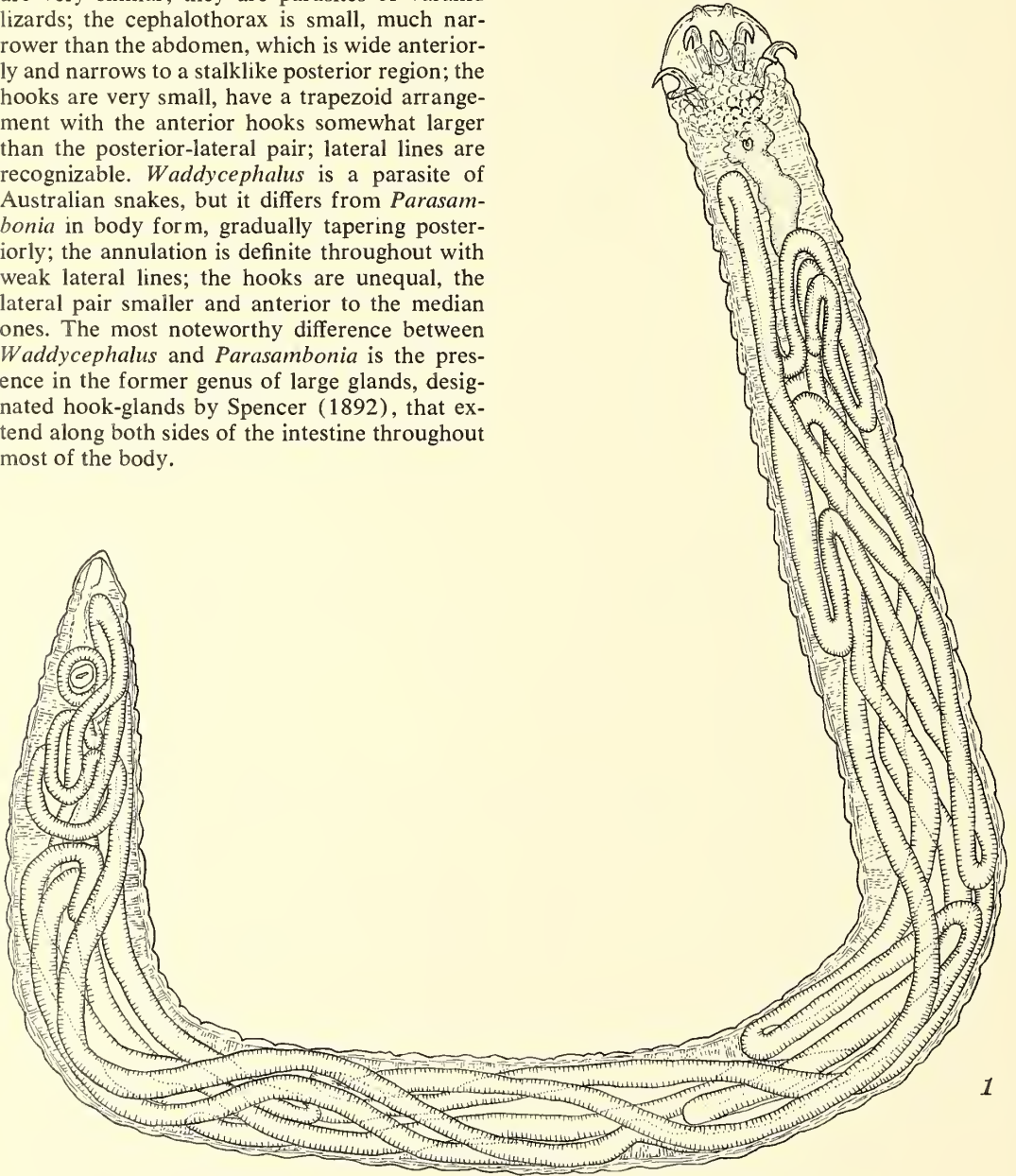


FIG. 1. Holotype, stained and mounted, ventral view, *Parasambonia bridgesi*.

length and 1.57 to 2.00 mm. in width. The abdomen is annulate but the annuli are often indistinct, especially at the posterior end and in regions where pressure from distended uterine loops obliterates the annulation. There is a slightly narrower region, comprising six to eight annuli, posterior to the cephalothorax and in the remainder of the abdomen, except for the caudal tip, the sides are almost parallel. The annuli in the anterior constricted region are about 1.57 mm. wide and 0.30 mm. long; throughout most of the body they are 1.65 to 1.90 mm. wide and 0.43 to 0.48 mm. long. In the specimen shown in Text-figure 1, the annulus that bears the uterine pore is 1.20 mm. wide and 0.25 mm. long. The posterior end of the body may be rounded or tapered to the tip. The terminal annulus has a slight dorsoventral cleft and the anus is located ventrally at the base of the cleft. As noted, in parts of the body the annuli are not distinct and in the region posterior to the uterine pore, 1.30 to 1.80 mm in length, the number could be determined in only two specimens. Although the total number could not be counted with certainty, there are about 60 annuli. Apparently the number varies slightly in different specimens.

No respiratory, circulatory, or excretory organs were recognized. The body cavity is a haemocoel; it contains a homogeneous fluid lacking cellular elements. Movement of the blood is effected by regional contractions of the general musculature. Throughout most of its length, the body cavity is occupied by loops of the uterus. Lateral lines, described for related species, were not observed. The cuticula measures 0.018 to 0.026 mm in thickness; it rests on a single layer of hypodermal cells. Scattered among the hypodermal cells on the dorsal and lateral sides of the head region, there are numerous, small, multicellular glands, the "Hautdrüsen" or "Stigmen-drüsen" of German authors. In addition, an irregular, staggered row of these glands (Text-fig. 2) extends around the annuli in most of the abdomen. They are often inconspicuous and apparently are absent near the posterior end of the body. In number and arrangement they are similar to those of *Sebekia oxycephala* as represented in Heymons (1935, Fig. 11). They vary from 0.030 to 0.045 mm. in diameter, with a transparent rim and a deeply staining core, some 0.010 mm. in diameter, which may be a central duct filled with secretion. These glands are bathed by the haemolymph of the body cavity and their function is still uncertain. The cuticula is turned in and lines the stomodeum, the procotodeum, the terminal portion of the uterus, and the pockets in which the hooks are located.

The cephalothorax is flattened ventrally and

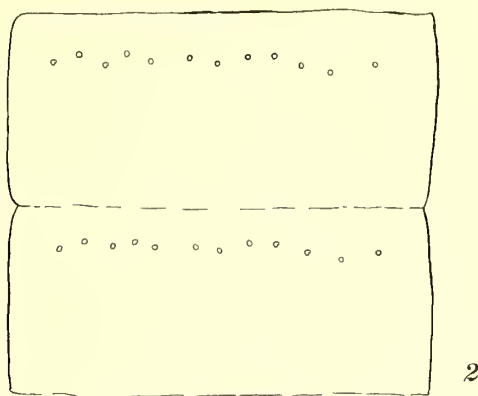


FIG. 2. Dermal glands on annuli, *Parasambonia bridgesi*.

from a lateral or ventral aspect, two annuli appear to be covered by or incorporated into it. It measures 1.60 to 1.90 mm. in width and 0.75 mm. to 1.20 mm. in length. The head is domed dorsally; the cuticula and hypodermis are separated from the underlying structures and the intervening region is large haemal sinus, which in fixed specimens is filled with a mass of coagulated body fluid. The anteroventral portion of the cephalothorax contains the muscular complex that operates the hooks. The hooks (Text-fig. 3) are simple, equal in shape and size, with the lateral hooks situated slightly posterior to the

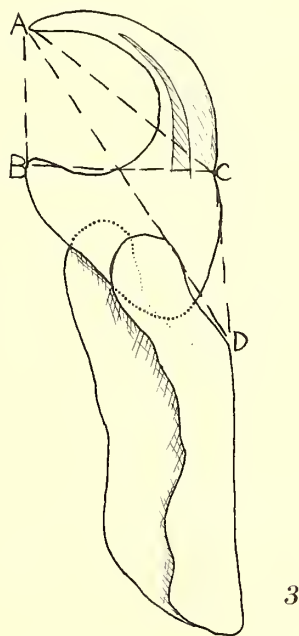


FIG. 3. Hook, *Parasambonia bridgesi*.

median ones. A scheme for measurements of the hooks was devised by Fain (1961). The measurements, as denoted in Text-figure 3, are: AB, 0.14 to 0.15 mm.; AC, 0.28 to 0.33 mm.; BC, 0.21 to 0.25 mm.; AD, 0.32 to 0.37 mm.; CD, 0.18 to 0.21 mm. The measurements AD and CD vary as the hook turns on the fulcrum. The fulcrum is 0.48 to 0.52 mm. long; it is concave ventrally, with two ventrolateral prongs that articulate on either side with the lateral base of the hook. Protractor muscles inserted on the hook at B and retractors inserted at C operate the rotary movements of the hook. Other muscles, inserted on the base of the hook and on the fulcrum, determine the position and orientation of the hook in the cephalothorax.

The anteroventral face of the cephalothorax bears two papillae, the "Tastpapillen" of Leuckart (1860), the "Sinnespapille A" of Haffner (1926) and the "Frontalpapillen" of Heymons (1935). They appear as protrusions of the body wall, anterior to and midway between the mouth and median hooks. In sections, they are pyriform, wider internally, 0.017 mm. long and 0.011 mm. wide, and resemble the "Papille A" of *Porocephalus clavatus* as figured by Haffner

(1926). The tip of the papilla bears a row of sensory cells, supplied by a nerve from the ganglion of that side, and contains the opening of a duct, 0.026 mm. in diameter, lined with low cuboidal epithelium, that extends dorsad and posteriad, lateral to the median sinus and above the musculature of the hooks. The duct appears to subdivide and terminate among the secretory cells located dorsal and lateral to the esophagus and the neural ganglia.

The paired ganglia (Text-fig. 4) are ventral, situated immediately posterior to the mouth. Each is 0.08 to 0.09 mm. in lateral and 0.06 to 0.07 mm. in dorsoventral measurements, and a commissure from the anterior part of the ganglia passes dorsally around the esophagus. Paired nerves extend from the ganglia to cephalic structures and a principal midventral pair extends posteriad through the length of the body. In the dorsolateral region, posterior to the esophagus and anterior to the intestine there are masses of secretory cells, each 0.06 to 0.08 mm. in diameter, with nuclei that measure 0.016 to 0.02 mm. in diameter and contain nucleoli that stain deeply. These cells appear comparable to the "Kopfdrüsen," "Frontal-



FIG. 4. Cross section through the subesophageal ganglia, *Parasambonia bridgesi*.

drüsen," or "Hakendrüsen" of Heymons (1935) and other authors. The function of these glands is problematical and the same is true of the so-called "Parietaldrüsen," occasional small groups of glandular cells situated along the abdomen between the somatic musculature and the body wall.

The mouth is situated between the median hooks, 0.50 to 0.60 mm. from the anterior end of the body. It is oval, longer in the anteroposterior axis; the opening varies from 0.08 by 0.16 to 0.12 by 0.23 mm. The mouth is situated in a cuticular frame, (Text-fig. 5), 0.41 to 0.48 mm. long and 0.21 to 0.25 mm. in greatest width. The pharynx, dorsal to the mouth and the esophagus, lined with cuticula, extends posteriorly above the ganglia to open into the intestine in the third or fourth annulus. The intestine is straight, leading to the anus at the posterior end of the body, but the wall of the gut has many large, internal folds (Text-fig. 6).

The ovary is a flattened tubular structure with lateral wings. It is supported by a mesentery and applied to the dorsal surface of the intestine. It begins a short distance anterior to the uterine pore, near the level of the middle of the metraterm, and extends to the fourth annulus from the anterior end of the body. Here paired oviducts pass ventrad on either side of the body and join in a wide tubular structure that receives ducts from the two seminal receptacles. The receptacles are oval, 0.60 to 0.75 mm. long and 0.45 to 0.54 mm. wide. They are situated on opposite sides of the body and may

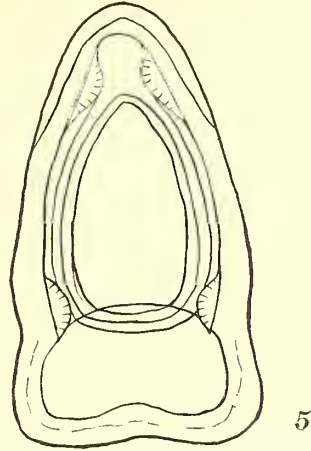


FIG. 5. Circumoral cuticular frame, *Parasambonia bridgesi*.

be at the same level or one may be anterior to the other. After fertilization, the eggs pass into the uterus. The uterus has a thin membranous wall and is disposed in many loops (Text-figs. 1, 6). The uterine pore is situated on the ventral surface of the sixth annulus from the posterior end of the body. The terminal portion of the uterus, comparable to the metraterm of the digenetic trematodes, is constricted, has a strong muscular wall consisting of outer circular and inner longitudinal fibers, and has a cuticular lining. It extends anteriorly from the uterine pore for 0.70 to 0.80 mm., where it becomes continuous with the last thin-walled

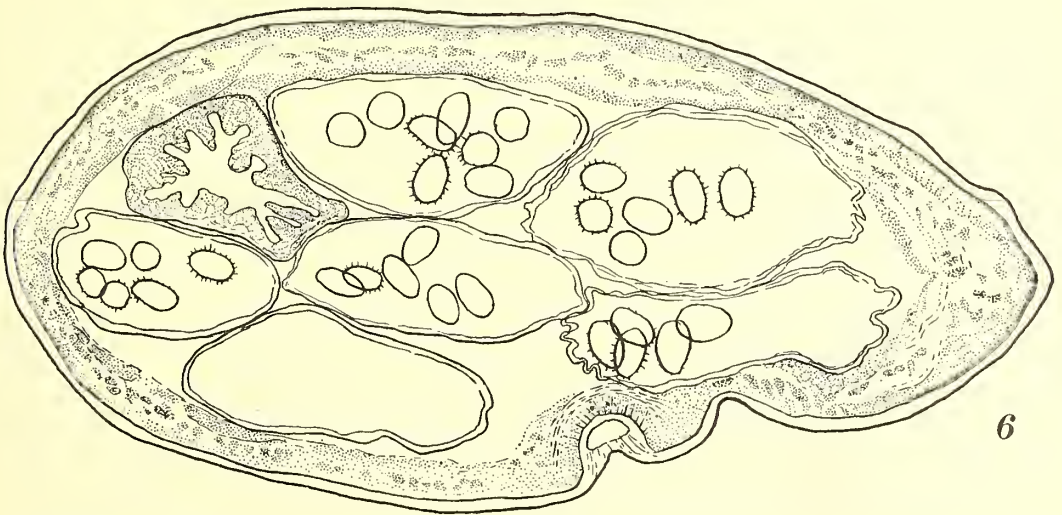


FIG. 6. Cross section through the uterine pore, showing eggs, uterine coils at this level, and folded wall of the intestine, *Parasambonia bridgesi*.

loop of the uterus, which turns posteriad to the level of the pore and then crosses to the opposite side of the body, where it loops posteriad. Newly formed eggs are oval, have smooth shells, are remarkably uniform in size, and average 0.055 by 0.038 mm. The shells of older eggs (Text-fig. 6) are 0.074 by 0.052 mm. and are covered by cylindrical projections, 0.005 to 0.007 mm. long, which appear to be embedded in a transparent matrix with a delicate membranous covering. Eggs in the terminal portion of the uterus contain fully formed larvae.

Type depositary: American Museum of Natural History, holotype No. 12924; paratypes: whole mounts and sections No. 12925; specimens in alcohol, 12926.

DISCUSSION

The first comprehensive study of the morphology and life cycle of the pentastomes was made by Leuckart (1860). He demonstrated that *Pentastomum denticulatum* (Rudolphi, 1809) Rudolphi, 1819, is the larval stage of *Pentastomum taenioides* (Rudolphi, 1809) Rudolphi, 1819, and that both are identical with *Linguatulida serrata* Fröhlich, 1789. In a footnote, Leuckart (1860, p. 2), noted that several helminthologists, including von Nordmann and van Beneden, had employed the generic name *Linguatula* Fröhlich, 1789, which he conceded was correct and in accord with the law of priority. But, influenced by the prestige of Rudolphi, German investigators had assigned species to the genus *Pentastomum* Rudolphi, 1819, and since the majority of named species had been described as members of *Pentastomum*, Leuckart adopted the name, although it is a junior synonym of *Linguatula*.

Classification: The classification of the pentastomes is based largely on the work of Sambon and Heymons, with a revision by Fain (1961). In early literature the tongue-worms, as they were called, were included in the family Linguatulidae and comprised three genera: *Linguatula* Fröhlich, 1789, *Porocephalus* Humboldt, 1809, and *Pentastoma* Rudolphi, 1819. In a contribution published in two parts, Sambon (1922a, June 15; 1922b, December 15) made extensive additions to knowledge of these parasites. He (1922a) divided the family Linguatulidae into two subfamilies: Raillietiellinae, based on *Raillietiella* Sambon, 1910, and Porocephalinae n. subf., based on *Porocephalus* Humboldt, 1809. The genus *Linguatula* was placed in the subfamily Porocephalinae, an obvious error, since it was the nomenclatural type of the family and must be type of the subfamily to which it is assigned. The two subfamilies

recognized by Sambon are morphologically distinct, and Sambon noted that in the Raillietiellinae the hooks are borne on stumplike protrusions of the body wall; the female genital pore is near the anterior end of the abdomen; the uterus is straight and sacciform; and the larva has six short, stumpy legs. In the subfamily Porocephalinae, on the other hand, the hooks are sessile; the female genital pore is at or near the posterior end of the body; the uterus is tubular, elongate, with numerous windings; and the larva has four legs. Sambon transferred several species to *Raillietiella* and included the genus *Reighardia* Ward, 1899, in the subfamily Raillietiellinae. The Porocephalinae were divided into three sections: I. Sebekini, with the genera *Sebekia* Sambon, 1922; *Alofia* Giglioli, 1922; and *Leiperia* Sambon, 1922; II. Porocephalini with the genera *Porocephalus* Humboldt, 1809; *Kiricephalus* Sambon, 1922; *Armillifer* Sambon, 1922; and *Waddycephalus* Sambon, 1922; III. Linguatulini with the genera *Linguatula* Fröhlich, 1789, and *Subtriquetra* Sambon, 1922.

Noc and Giglioli (1922) erected the genus *Sambonia* to contain *Pentastomum clavatum* Lohrmann, 1889, a species that had been included in the genus *Sebekia* by Sambon (1922a). In a paper published on October 27, Heymons (1922) described *Raillietiella mabuiae* and erected a new genus, *Cephalobaena*, to receive a new species, described as *Cephalobaena tetrapoda*, taken from South American snakes. He included *Cephalobaena* and *Raillietiella* in a new family, Cephalobaenidae. But *Raillietiella* had been named as a type of the subfamily Raillietiellinae by Sambon (1922a), and since the name of the family and type subfamily must be formed from the name of the type genus, the family name must be Raillietiellidae, and Cephalobaenidae is a subjective synonym. Sambon (1922b) suppressed *Cephalobaena* as a synonym of *Raillietiella*, discussed previously described species, and compiled a list of the Linguatulidae, arranged according to classification, definitive hosts, and geographical distribution.

Heymons (1935) published a comprehensive treatise on the Pentastomida and presented a revised system of classification. The group was accorded the taxonomic status of a class. He noted that the two names, Pentastomida and Linguatulida, were equally available; and although *Linguatula* antedates *Pentastoma*, he chose to follow Leuckart and adopted Pentastomida as the name for the class, because Rudolphi had formulated a concept of the group, whereas Fröhlich merely described a larva

from the lungs of the hare. Rudolphi's concept of the group was vague, however, since he included *Pentastomum* in the Trematoda, between *Polystomum* and *Tristomum* on the mistaken belief that the hooks of the pentastomes were comparable to the suckers and hooks of the pectobothriid trematodes, which at the time were believed to be anterior in position. Comparison with other invertebrate groups led Heymons to the conclusion that the pentastomes were derived from annelidlike progenitors; moreover, their morphology and distribution suggested an isolated and phylogenetically ancient group, probably parasitic in extinct paleozoic reptiles. In a recent study, Osche (1963) reaffirmed the arthropod affinities of the pentastomes.

In the class Pentastomida, Heymons (1935) recognized two orders: Cephalobaenida, with two families, Cephalobaenidae and Reighardiidae; and Porocephalida, with two families, Porocephalidae and Linguatulidae. Since suprafamilial names are not subject to the rules that apply to family names, the order Cephalobaenida is acceptable, but as noted earlier, if *Raillietiella* and *Cephalobaena* are in the same subfamily, the name of the family must be Raillietiellidae. The family Reighardiidae contained only the genus *Reighardia*. In the family Porocephalidae, Heymons recognized four subfamilies: I. Porocephalinae with five genera; *Porocephalus* Humboldt, 1809; *Armillifer* Sambon, 1922; *Kiricephalus* Sambon, 1922; *Waddycephalus* Sambon, 1922; and *Ligamifer* Heymons, 1932. II. Sebekinae with three genera; *Sebekia* Sambon, 1922; *Leiperia* Sambon, 1922; and *Alofia* Giglioli, 1922. III. Diesinginae with two genera; *Diesingia* Sambon, 1922; and *Elenia* Heymons, 1932. IV. Samboninae, new subfamily, to receive *Sambonia* Noc and Giglioli, 1922. The family Linguatulidae contained two genera: *Linguatula* Fröhlich, 1789, and *Subtriquetra* Sambon, 1922. The two orders recognized by Heymons are virtually identical with the two subfamilies of Sambon (1922a). Heymons (1940) noted the agreement between *Sambonia* and *Elenia* and suggested that the two may be identical. In a later report, Heymons (1941a, p. 323) stated "Die drei Gattungen, *Sambonia*, *Elenia* und *Waddycephalus* stehen einander sehr nahe." Further comparison led to the conclusion that the two genera, *Sambonia* and *Elenia* should be retained and four genera, *Sambonia*, *Elenia*, *Waddycephalus*, and *Ligamifer*, were characterized. The subfamily Samboninae was elevated to family status to contain the first three genera. Relationship of *Ligamifer* to the genus *Armillifer* was noted

with the comment (Heymons, 1941a, p. 325), "Wo der Trennungsstrich zwischen Sambodiden und Armilliferiden zu ziehen ist, wissen wir noch nicht."

In a revision, Fain (1961) retained the two orders Cephalobaenida and Porocephalida. Cephalobaenida contained two families: Cephalobaenidae and Reighardiidae. The Cephalobaenidae contained three genera: *Cephalobaena* with a single species; *Raillietiella* with 19 species arranged in five groups; and *Megadrepanoides* Self and Kuntz, 1957, with two species. The order Porocephalida was divided into two suborders: Porocephaloidea and Linguatuloidea. The Linguatuloidea contained the single family Linguatulidae and the single genus *Linguatula*. The suborder Porocephaloidea contained five families: Porocephalidae, Sebekidae, Armilliferidae, Sambonidae, and Subtriquetridae, a new family, to receive the genus *Subtriquetra*, which was transferred from the Linguatulidae. The family Sambonidae contained three genera: *Sambonia*, *Elenia*, and *Waddycephalus*. Fain noted that infection by two different species of pentastomes is a rare occurrence. It is interesting also to note that with the exception of two genera—*Reighardia*, whose only species occurs in birds; and *Linguatula*, with species only in mammals—all other pentastomes are parasites of reptiles. Larval stages occur in fishes and mammals, but specimens become adult only in amniotes.

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Eastern Pacific Expeditions of the New York Zoological Society.
Porcellanid Crabs (*Crustacea: Anomura*) from the
West Coast of Tropical America

JANET HAIG

*Allan Hancock Foundation
University of Southern California*

(Text-figures 1 & 2)

[This is the forty-seventh of a series of papers dealing with the collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of William Beebe. The present paper is concerned with specimens taken on the Templeton Crocker Expedition (1936) and the Eastern Pacific *Zaca* Expedition (1937-1938). For data on localities, dates, dredges, refer to *Zoologica*, Vol. XXII, No. 2, pp. 33-46, and Vol. XXIII, No. 14, pp. 287-298.]

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INTRODUCTION

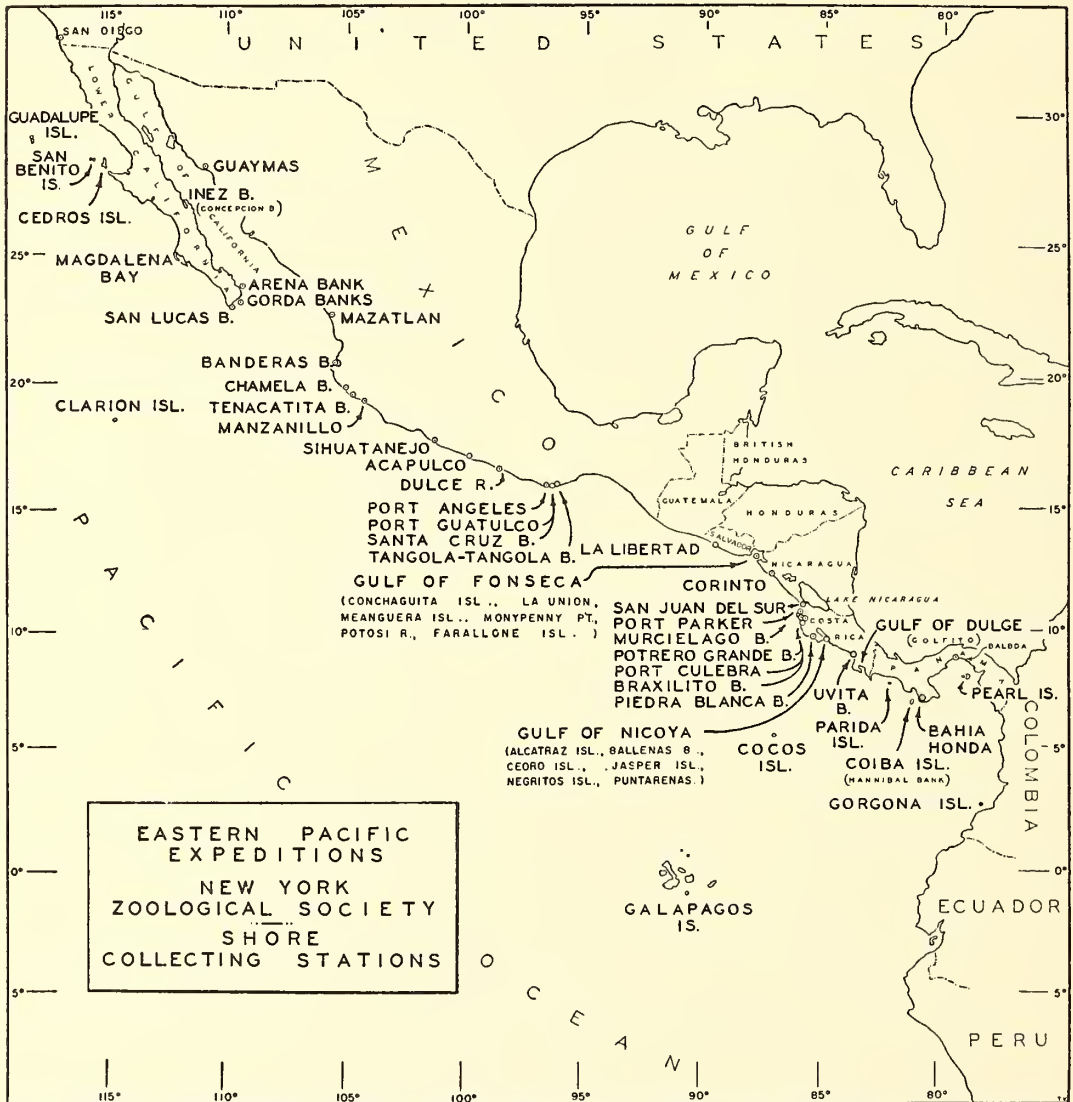
DURING a three-year period, 1936 to 1938, two expeditions sponsored by the New York Zoological Society and under the direction of Dr. William Beebe explored the west coast of tropical America aboard the yacht *Zaca*. The first, the Templeton Crocker Expedition (1936), covered the west coast of Baja California, the southern half

of the Gulf of California, and Clarion Island of the Revillagigedo group; the second, the Eastern Pacific *Zaca* Expedition (1937-1938), proceeded along the coast of Mexico and Central and South America as far south as Gorgona Island, Colombia. (See Text-fig. 1.)

The porcellanid crabs from the 1936 Templeton Crocker Expedition (with the exception of those collected at Clarion Island) were the subject of a report by Glassell (1937). While preparing a monograph on the Porcellanidae of the eastern Pacific, I had hoped to examine

material of that family obtained during the expedition of 1937-1938; at that time, however, it was packed away and not accessible for study, except for a few lots, which were examined and subsequently incorporated in the monographic treatment (Haig, 1960) along with specimens collected at Clarion Island during the 1936 expedition.

The bulk of the porcellanids from the Eastern Pacific *Zaca* Expedition (1937-1938) has since become available for examination, and all the Porcellanidae collected during that ex-



TEXT-FIG. 1. Shore collecting stations of the Eastern Pacific Expeditions of the New York Zoological Society. For exact locations of associated dredge stations, refer to *Zoologica*, vol. XXII, no. 2, and vol. XXIII, no. 14.

pedition form the subject matter of the present report. In general, the style of presentation follows that of Garth (1959, 1961, 1966), who reported on part of the brachyuran crabs collected by the expedition, the intertidal brachygnaths having been dealt with earlier by Crane (1947).

The material has been deposited in the American Museum of Natural History; in this report the AMNH catalog number referring to each lot is indicated in parentheses. A few specimens from the group studied before 1960 were donated to the Allan Hancock Foundation, and these are identified (AHF) in the text.

ECOLOGICAL CONSIDERATIONS

Porcellanid crabs are usually conspicuous members of the coral community in tropical seas. Most species are not obligate commensals with corals, but may be found in a variety of habitats that offer concealment. Nevertheless certain species are predominantly coral dwellers and have only rarely been found in other situations: in the eastern Pacific these include *Petrolisthes glasselli*, *Petrolisthes polymitus*, *Pachycheles biocellatus*, *Pachycheles vicarius*, and several others. Some species, on the other hand, are generally found under stones in the littoral or have been dredged from various kinds of substrates, but occasionally turn up among crabs and other animals taken from coral heads. *Petrolisthes edwardsii* and *Pisidia magdalenensis* are examples.

Of the 36 species of porcellanids from the Eastern Pacific Zaca Expedition, 18, or 50 per cent, were collected from corals. Crane (1947, pp. 88-89) reported that "More than 50 heads of coral, ranging in diameter from six inches to more than two feet, were carefully hammered open and their inhabitants collected." The best locality for this type of collecting, as far as the Porcellanidae were concerned, was Sihuate-nejo Bay, where 14 species were recovered from corals in the intertidal zone. Eleven species were collected from intertidal corals at Jasper Island; ten at Uvita Bay; at least nine at Port Parker; and eight at Port Culebra. At Port Guatulco, eight species were found in corals obtained by diving in 1½ fathoms.

Crane (1947, p. 87) enumerated nine habitat zones for the intertidal brachygnathous Brachyura of the 1937-1938 expedition. *Petrolisthes zaca*, described herein, was found living on mud among mangroves; otherwise the coral habitat zone was the only one specified for the Porcellanidae of the expedition. Thirteen species not collected in the latter zone were probably

from "stones near midtide levels," "stones near low-tide levels," or "tidepools."

Dredged species included *Petrolisthes robsonae* and *Polyonyx confinis*, from mud and mangrove leaves in 3 fathoms; and *Porcellana cancrisocialis*, *Porcellana paguriconviva*, and *Pisidia magdalenensis*, chiefly on sand, mud, crushed shell, and rock substrates in 2½ to 30 fathoms.

Among the species collected was an obligate commensal, *Minyocerus kirki*, which lives in association with sea stars and serpent stars. *Porcellana cancrisocialis* and *Porcellana paguriconviva*, free-living over a rather wide bathymetric range, are frequently found with various species of large hermit crabs in their shells; three *P. paguriconviva* from the Eastern Pacific Zaca Expedition were associated with a hermit crab of unknown identity.

GEOGRAPHICAL CONSIDERATIONS

As a result of the present study, the known range of *Pachycheles crassus* is extended from Balboa, Panama, to Sihuate-nejo Bay, Mexico. Smaller northward range extensions include *Petrolisthes tridentatus* from Salinas Bay, Costa Rica, to San Juan del Sur, Nicaragua; and *Pachycheles calculosus* and *Megalobrachium festai* from Acapulco to Sihuate-nejo Bay, Mexico. *Petrolisthes robsonae* is reported from La Union, El Salvador, the first precise locality for the species north of Panama although it was recorded earlier from an unspecified area in Mexico. *Petrolisthes galapagensis* is reported from the Gulf of Nicoya, Costa Rica, the first mainland record for the species.

Petrolisthes lewisi is recorded from the Gulf of California south to Ecuador, but with a wide gap in its known distribution. Since the two populations in this discontinuous range are recognized as subspecies, it may be assumed that they meet somewhere in the intermediate area, which is now narrowed with the extension of *Petrolisthes lewisi lewisi* southward from Tequepa Bay to Tangola-Tangola Bay, Mexico, and of *P. l. austrinus* northward from Salinas Bay, Costa Rica, to the Gulf of Fonseca.

In the present report, several species are noted for the first time from certain countries visited by the Zaca. These records may be listed as follows:

New to Mexico: *Pachycheles crassus*.

New to El Salvador: *Petrolisthes robsonae*.

New to Nicaragua: *Petrolisthes agassizii*, *P. edwardsii*, *P. nobilii*, *P. tridentatus*, *P. tonsorius*, *P. lewisi austrinus*, *Neopisosoma mexicanum*, and *Pachycheles trichotus*.

New to Costa Rica: *Petrolisthes galapagensis*, *Pachycheles chacei*, *Megalobrachium garthi*, and *M. tuberculipes*.

SYSTEMATIC CONSIDERATIONS

Two new species, neither of which is yet known from any other source, are represented in the collection of Porcellanidae from the Zaca Expedition (1937-1938). One of these, *Polyonyx confinis*, has already been treated (Haig, 1960); the other, *Petrolisthes zacae*, is described in the present report.

Sixty-five eastern Pacific porcellanid species are now recognized as members of the Panamic faunal province, which extends from the head of the Gulf of California to the Gulf of Guayaquil, Ecuador, and includes a number of outlying islands. Of these tropical species, fifteen appear to be restricted to the Gulf of California or to the Cocos and Galapagos Islands, areas not visited by the Zaca. The expedition obtained 36 of the remaining 50 species, or 72 per cent of the total.

RESTRICTION OF SYNONYMIES

For each species a reference is given to the recent revision of eastern Pacific Porcellanidae (Haig, 1960), which may be consulted for all earlier references. Pertinent works published since 1960 are also cited. Otherwise, the synonymies are restricted to the following references: the work containing the original description of the species; that first citing the name in its present combination; and those containing the original descriptions of its junior synonyms. For *Petrolisthes armatus* and *Megalobrachium poeyi*, species that occur in the Atlantic Ocean as well as the Pacific, junior synonyms with an Atlantic coast type locality are not cited.

SYSTEMATIC DISCUSSION

Family PORCELLANIDAE

Petrolisthes agassizii Faxon

Petrolisthes agassizii Faxon, 1893, p. 174. Haig, 1960, pp. 24, 32, pl. 20 fig. 4; 1962, p. 174.

Range.—From Mazatlan, Gulf of California, to Utria Bay, Colombia. Shore to 5 fathoms.

Material Examined.—17 specimens from 4 stations:

Mexico

Tangola-Tangola Bay, December 8-13, 1937, intertidal in coral, 1 male (12596).

Nicaragua

Corinto, December 28, 1937-January 7, 1938, intertidal, 1 male, 3 females (12597).

Costa Rica

Port Parker, January 12-23, 1938, intertidal 1938, 6-2½ fathoms, rocks, 5 males, 6 females (12598).

Port Parker, Station 203, D-10, January 22, 1938, 6-2½ fathoms, rocks, 5 males, 6 females (12598).

Measurements.—Males 5.3-6.5 mm., ovigerous females 6.1-8.5 mm.

Breeding.—Ovigerous females from Corinto in late December or early January, and from Port Parker in late January.

Remarks.—The male specimen collected intertidally at Port Parker was reported by Haig (1960, p. 257).

Petrolisthes edwardsii (Saussure)

Porcellana edwardsii Saussure, 1853, p. 366, pl. 12 fig. 3.

Petrolisthes edwardsii Stimpson, 1858, p. 227. Haig, 1960, pp. 24, 33, pl. 21; 1962, p. 175.

Range.—From Santa Maria and Magdalena Bays, outer Baja California, and Los Frailes, Gulf of California, to La Plata Island, Ecuador. Isabel, Tres Marias, Revillagigedo, and Galapagos Islands. Shore to 20 fathoms.

Material Examined.—53 specimens from 12 stations:

Mexico

Chamela Bay, November 17-20, 1937, intertidal, 3 males (12599).

Tenacatita Bay, November 20, 1937, intertidal, 4 males, 5 females, 3 young (12600).

Sihuatenejo Bay, November 24, 1937, intertidal in coral, 2 females, 1 young (12601).

Port Angeles, December 1, 1937, intertidal, 3 males, 2 females (12602).

Port Guatulco, Station 195, D-15, December 6, 1937, diving in 1½ fathoms, coral, 1 young male, 2 young females, 2 young (12603).

Tangola-Tangola Bay, December 8-13, 1937, intertidal in coral, 2 males (1 young), 1 female (12604).

Nicaragua

Corinto, December 28, 1937-January 7, 1938, intertidal, 2 females (12605).

Costa Rica

Port Parker, January 12-23, 1938, intertidal (in coral?), 9 males, 4 females (11788).

Port Parker, Station 203, D-10, January 22, 1938, 6-2½ fathoms, rocks, 2 females (12606).

Port Culebra, January 24-31, 1938, intertidal from coral, 1 female (12607).

Jasper Island, Gulf of Nicoya, February 22-25, 1938, intertidal in coral, 1 male (12608).

Panama

Bahia Honda, March 13-19, 1938, low tide under stones, 3 males (12609).

Measurements.—Males 3.8-12.0 mm., nonovigerous females 4.2-8.6 mm., ovigerous females 5.3-10.0 mm.

Breeding.—Ovigerous females from Tenacatita and Sihuatenejo Bays in November, from Corinto in late December or early January, and from Port Parker and Port Culebra in January.

Remarks.—A specimen from Chamela Bay is parasitized by a bopyrid. The material collected intertidally at Port Parker was recorded by Haig (1960, p. 258).

***Petrolisthes glasselli* Haig**

Petrolisthes glasselli Haig, 1957a, p. 33, pl. 8 figs. 1-3; 1960, pp. 24, 39, pl. 20 fig. 2; 1962, p. 176. Chace, 1962, p. 623.

Range.—From Cape San Lucas, Gulf of California, to Gorgona Island, Colombia. Isabel, Tres Marias, Revillagigedo, Galapagos, and Clipperton Islands. Shore to 4 fathoms.

Material Examined.—284 specimens from 5 stations:

Mexico

Sihuatenejo Bay, November 24, 1937, intertidal in coral, 1 male, 3 females (12610).

Port Guatulco, Station 195, D-15, December 6, 1937, diving in 1½ fathoms, coral, 1 male, 1 female (12611).

Costa Rica

Port Parker, January 12-23, 1938, intertidal (in coral?), 97 males, 121 females, 39 young (11786).

Port Culebra, January 24-31, 1938, intertidal in coral, 4 young (12612).

Uvita Bay, March 2-4, 1938, intertidal in coral, 8 males, 9 females (12613).

Measurements.—Males 4.1-10.0 mm., nonovigerous females 4.0-7.8 mm., ovigerous females 5.2-9.6 mm.

Breeding.—Ovigerous females from Sihuatenejo Bay in November, from Port Guatulco in December, from Port Parker in January, and from Uvita Bay in March.

Remarks.—This species, which has rarely been found except in association with corals, is the only eastern Pacific *Petrolisthes* with two epi-branchial spines on either side of the carapace.

The specimens from Port Parker were previously reported by Haig (1960, p. 262).

***Petrolisthes polymitus* Glassell**

Petrolisthes polymitus Glassell, 1937, p. 81, pl. 1

fig. 1. Haig, 1960, pp. 25, 41, pl. 22 fig. 1; 1962, p. 176.

Range.—From Espiritu Santo Island, Gulf of California, to La Libertad, Ecuador. Tres Marias and Galapagos Islands. Shore to 4 fathoms.

Material Examined.—13 specimens from 4 stations:

Mexico

Sihuatenejo Bay, November 24, 1937, intertidal in coral, 1 female (12614).

Port Guatulco, Station 195, D-15, December 6, 1937, diving in 1½ fathoms, coral, 2 males, 5 females (12615).

Costa Rica

Jasper Island, Gulf of Nicoya, February 22-25, 1938, intertidal in coral, 2 males, 1 female (12616).

Uvita Bay, March 2-4, 1938, intertidal in coral, 1 male, 1 female (12617).

Measurements.—Males 4.0-5.0 mm., nonovigerous female 4.8 mm., ovigerous females 3.3-4.9 mm.

Breeding.—Ovigerous females from Sihuatenejo Bay in November, from Port Guatulco in December, from Jasper Island in February, and from Uvita Bay in March.

Remarks.—This species was originally described from a single specimen collected in the Gulf of California during the 1936 Templeton Crocker Expedition. It was taken over a wide geographical area during various cruises of *Velero III* and *Velero IV*.

***Petrolisthes haigae* Chace**

Petrolisthes marginatus, Haig, 1960, pp. 25, 47, pl. 20 fig. 1. Not *P. marginatus* Stimpson.

Petrolisthes sp., Haig, 1962, p. 177.

Petrolisthes haigae Chace, 1962, p. 620, text-fig. 1.

Range.—From Guaymas Bay, Gulf of California, to Santa Elena Bay, Ecuador. Isabel, Tres Marias, Revillagigedo, Galapagos, and Clipperton Islands. Shore to about 10 fathoms (exceptionally to 22 fathoms).

Material Examined.—525 specimens from 10 stations:

Mexico

Tenacatita Bay, November 20, 1937, intertidal, 1 female (12618).

Sihuatenejo Bay, November 24, 1937, intertidal in coral, 14 males, 26 females (12619).

Acapulco, November 25-29, 1937, intertidal, 2 males, 7 females (12620).

Port Guatulco, Station 195, D-14, December 6, 1937, 4 fathoms, coral, 1 male (12621); D-

15, December 6, 1937, diving in 1½ fathoms, coral, 21 males, 35 females, 1 young (12622).

Costa Rica

Port Parker, January 12-23, 1938, intertidal (in coral?), 110 males, 146 females (11780).

Port Parker, Station 203, D-9, January 22, 1938, 1½-4 fathoms, coral, 2 males, 1 young (12623).

Port Culebra, January 24-31, 1938, intertidal in coral, 90 specimens (12624).

Jasper Island, Gulf of Nicoya, February 22-25, 1938, intertidal in coral, 18 males, 13 females (12625).

Uvita Bay, March 2-4, 1938, intertidal in coral, 16 males, 17 females (12626).

Panama

Bahia Honda, March 13-19, 1938, low tide under stones, 1 male, 3 females (12627).

Measurements.—Males 2.6-9.5 mm., nonovigerous females 2.4-7.4 mm., ovigerous females 3.5-9.2 mm.

Breeding.—Ovigerous females from Tenacatita Bay, Sihuatenejo Bay, and Acapulco in November, from Port Guatulco in December, from Port Parker and Port Culebra in January, from Jasper Island in February, and from Uvita Bay and Bahia Honda in March.

Remarks.—This species occurs abundantly throughout its range. Chace (1962) showed that it is distinct from *Petrolisthes marginatus* Stimpson, a closely related west Atlantic form.

The specimens collected intertidally at Port Parker were reported by Haig (1960, p. 267) as *Petrolisthes marginatus* Stimpson.

Petrolisthes armatus (Gibbes)

Porcellana armata Gibbes, 1850, p. 190.

Petrolisthes armatus, Stimpson, 1858, p. 227.

Haig, 1960, pp. 25, 50, pl. 19 fig. 2; 1962, p. 178.

Range.—From Puerto Peñasco and San Felipe, Gulf of California, to Independencia Bay, Peru. Galapagos Islands. Shore to 10 fathoms. Also occurs in western and eastern Atlantic.

Material Examined.—32 specimens from 5 stations:

Nicaragua

Near Potosi River, Gulf of Fonseca, December 23-25, 1937, intertidal, 5 males, 7 females (12628).

Costa Rica

Port Parker, January 12-23, 1938, intertidal, 6 males, 7 females (12629).

Port Culebra, January 24-31, 1938, intertidal, 3 males (12630).

Cedro Island, Gulf of Nicoya, February 12-13 or 21-22, 1938, intertidal, 1 male, 1 female (12631).

Panama

Bahia Honda, March 13-19, 1938, low tide under stones, 1 male, 1 young female (12632).

Measurements.—Males 2.6-11.7 mm., nonovigerous females 3.9-5.5 mm., ovigerous females 4.5-7.3 mm.

Breeding.—Ovigerous females from Gulf of Fonseca in December, from Port Parker in January, and from Cedro Island in February.

Petrolisthes nobilii Haig

Petrolisthes nobilii Haig, 1960, pp. 25, 55, pl. 1, pl. 18 fig. 3.

Range.—From Cabeza Ballena, Gulf of California, to Santa Elena Bay, Ecuador. Isabel Island. Intertidal zone.

Material Examined.—16 specimens from 7 stations:

Mexico

Sihuatenejo Bay, November 24, 1937, intertidal under stones, 1 male (12633).

Port Angeles, December 1, 1937, intertidal, 1 female (12634).

Tangola-Tangola Bay, December 8-13, 1937, intertidal, 2 males, 2 females (12635).

Nicaragua

Corinto, December 28, 1937-January 7, 1938, intertidal, 1 male, 1 female (12636).

San Juan del Sur, January 9-12, 1938, intertidal, 2 males, 2 females (12637).

Costa Rica

Ballenas Bay, Gulf of Nicoya, February 25-26, 1938, intertidal, 1 female (12638).

Colombia

Gorgonilla Island, March 30, 1938, intertidal under rocks, 1 male, 1 female (12639).

Measurements.—Males 6.7-10.4 mm., nonovigerous female 4.3 mm., ovigerous females 5.6-10.4 mm.

Breeding.—Ovigerous females from Port Angeles and Tangola-Tangola Bay in December, from Corinto in late December or early January, from San Juan del Sur in January, from Ballenas Bay in February, and from Gorgonilla Island in March.

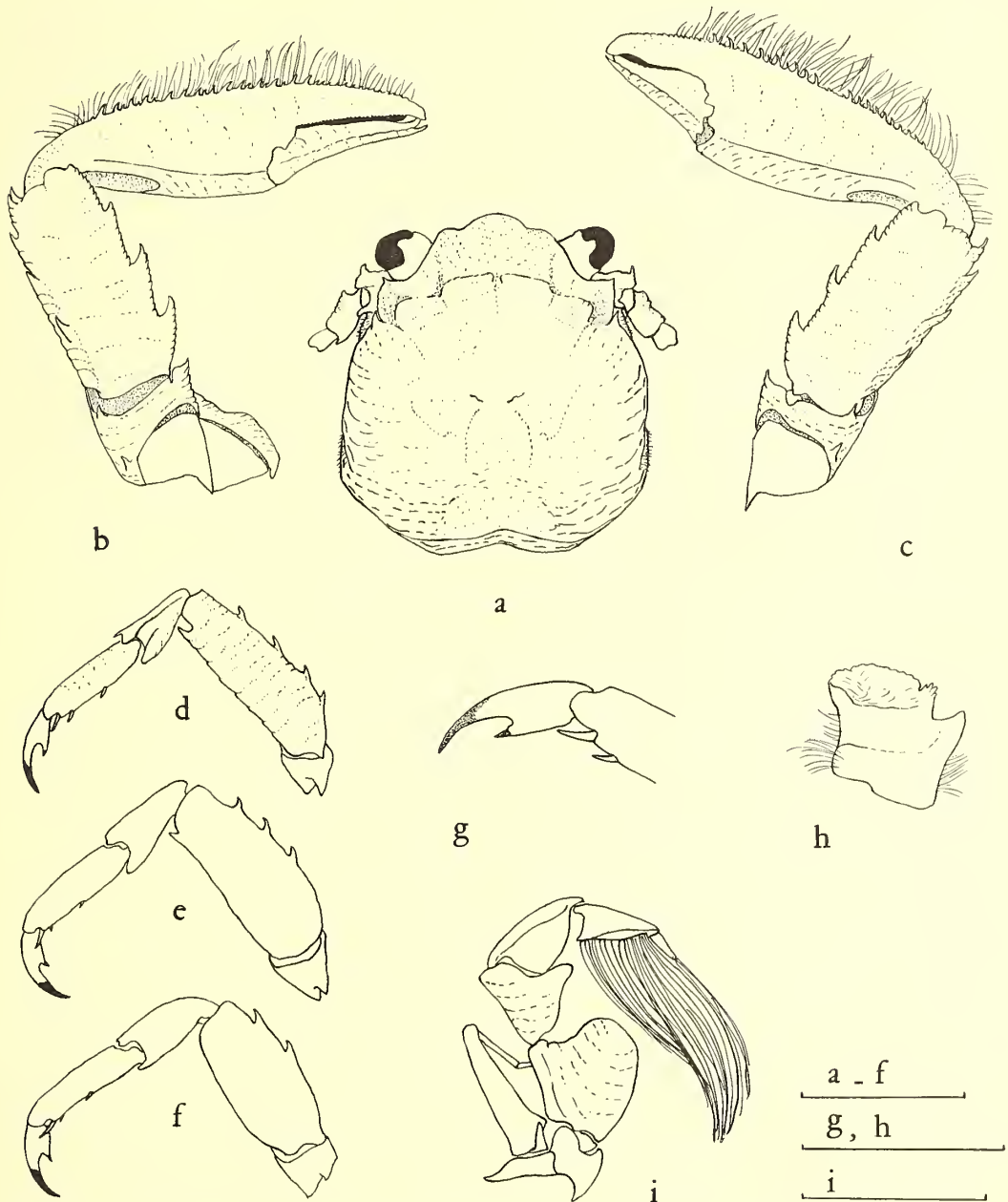
***Petrolisthes zacae*, new species**

(Text-fig. 2)

Types.—Female holotype, AMNH Cat. No. 12640, from Ballenas Bay, Gulf of Nicoya, Costa Rica, February 25 or 26, 1938, intertidal in mangrove mud. One male and one female, paratypes, AMNH Cat. No. 12641, same data as holotype.

Measurements.—Female holotype, length 8.6 mm., width 7.8 mm. Male paratype, length 5.0 mm. Ovigerous female paratype, length 7.8 mm.

Diagnosis.—Carapace finely rugose; no supraocular spine; a single epibranchial spine; front broad, with three shallow lobes. Carpus of chelipeds about two and a half times as long as wide, inner margin with three narrow, wide-set



TEXT-FIG. 2. *Petrolisthes zacae*. Holotype: a, carapace; b and c, chelipeds; d, e, and f, left walking legs 1, 2, and 3, respectively; g, dactyl of left first walking leg. Paratype: h, basal segment of right antennule; i, right third maxilliped. (Scale a-f = 4 mm.; g, h = 2 mm.; i = 3 mm.)

teeth, outer margin with four similar teeth; chela long and slender, its outer margin spinulate. Merus of walking legs with a few spines on upper margin; dactyl with a single movable spinule on lower margin.

Description.—Carapace finely rugose, especially along lateral and posterolateral margins; dorsal surface flat, regions not strongly indicated except for hepatics, which lie at a level below that of rest of carapace, and protogastric lobes. Front broad, flat or very faintly concave, with three shallow, rounded lobes, median one broader and more produced than laterals. No supraocular spine. Orbits shallow, strongly oblique; outer orbital angle subrectangular and sometimes produced into a minute spinule. A well-developed epibranchial spine. No hairs on dorsal surface of carapace; lateral portion with very short hairs.

a series of long, slender, rather evenly spaced spinules, more than 20 in number in the holotype, not developed on the proximal fourth of the palm nor on the outer margin of the pollex. Fingers smooth on dorsal surface, curved and crossing at tips; outer margin of dactyl with a ridge, produced into a sharp spinule at point where the finger curves sharply inward and crosses under pollex. A short, thick pubescence on lower inner side of fingers, on dactyl extending more than halfway to tip. Outer margin of chela with a fringe of very fine hairs, not obscuring row of spinules.

Walking legs transversely rugose, and with a few very fine, scattered hairs on margins. Merus with a posterodistal spine on legs 1 and 2, none on leg 3; anterior margin with a few spines (well-developed in female specimens, weakly developed in the small male), as follows in Table I:

TABLE I
SPINULATION OF WALKING LEGS

<i>Legs</i>	Holotype ♀ 8.6 mm.	Paratype ♀ 7.8 mm.	Paratype ♂ 5.0 mm.
Leg 1 (left)	4	3	2
Leg 1 (right)	3	3	2
Leg 2 (left)	3	3	2
Leg 2 (right)	3	(leg missing)	(leg missing)
Leg 3 (left)	2	(leg missing)	(leg missing)
Leg 3 (right)	2	(leg missing)	2

First movable segment of antenna with a strongly projecting, rounded, spine-tipped lamellar lobe; second granular, slightly produced at proximal end of anterior margin; third smooth; flagellum without hairs. Outer maxilliped and antennule as shown in Text-figure 2.

Chelipeds subequal. Merus lightly rugose; armed on inner margin with a strong pointed tooth; two spines on dorsal surface near outer margin, one at distal and the other near proximal end of segment. Carpus nearly two and a half times as long as wide; dorsal surface nearly smooth, evenly convex; armed on inner margin with three low, narrow, wide-set teeth (the most distal one not developed in the small male paratype), their edges finely crenulate; outer margin with four similar teeth, the most distal one bifid and placed at outer distal angle, the proximal two placed slightly on dorsal surface. Chela long and slender, smooth, evenly convex; outer margin crenulate, some of the crenulations in the form of short, close-set spinules; on dorsal surface just to the inside of the crenulated margin,

Carpus with anterodistal spine well developed on leg 1, obsolescent or absent on legs 2 and 3. Propodus long and slender; two movable spinules on lower margin in addition to the usual posterodistal pair. Dactyl long and slender; a "thumblike" projection about halfway along lower margin, tipped with a movable corneous spinule; lower margin otherwise unarmed. (The spinule and the corneous fixed claw are paler in color than indicated in Text-fig. 2 d-f.)

Remarks.—*Petrolisthes zacae* is allied to a small group of species, including *P. armatus* (Gibbes), *P. nobilii* Haig, and *P. robsonae* Glassell, in which the carapace is not transversely striate; there are low, wide-set teeth on the inner margin of the carpus of the cheliped; and the anterior margin of the merus of the walking legs is armed with only a few spines. It differs from all of them by a combination of several characters, and particularly by the form of the dactyl of the walking legs. As far as I am aware, the structure of the dactyl in this species is unique among porcellanids of genus *Petrolisthes*. Assuming

that the types were collected in a situation typical for the species, it is probably an adaptation for living in mud.

***Petrolisthes robsonae* Glassell**

Petrolisthes robsonae Glassell, 1945, p. 227, text-fig. 3. Haig, 1960, pp. 25, 57, pl. 18 fig. 2.

Range.—Mexico (specific locality not known) to Guayaquil, Ecuador.

Material Examined.—La Union, Gulf of Fonseca, El Salvador, Station 199, D-21, December 27, 1937, 3 fathoms, mud, mangrove leaves, 2 males, 1 female (12642).

Measurements.—Males 6.5 and 7.0 mm., nonovigerous female 5.3 mm.

Remarks.—An unusual characteristic of this species is its ability to withstand great changes in salinity (Haig, 1960, pp. 58-59). It has been collected at both ends of the Panama Canal, its occurrence on the Atlantic side of the Isthmus of Panama probably being due to an accidental introduction. It is also reported from Bellavista, Panama City; Guayaquil, Ecuador; and an unspecified locality in Mexico. With the discovery of specimens among the material collected by the *Zaca* during the 1937-1938 expedition, La Union becomes the northernmost precise locality known for the species.

***Petrolisthes gracilis* Stimpson**

Petrolisthes gracilis Stimpson, 1858, p. 227 (*nomen nudum*); 1859, p. 74. Haig, 1960, pp. 28, 79, pl. 27 fig. 2.

Range.—From Santa Maria Bay, Baja California, and Punta Peñasco and San Felipe, Gulf of California, to Tangola-Tangola Bay, Mexico. Tres Marias Islands. Shore; rarely to 25 fathoms.

Material Examined.—6 specimens from 3 stations:

Mexico

Sihuatenejo Bay, November 24, 1937, intertidal under stones, 1 male, 2 females (12643).

Port Guatulco, December 2-7, 1937, intertidal, 1 male (12644).

Tangola-Tangola Bay, December 8-13, 1937, intertidal, 2 males (12645).

Measurements.—Males 2.6-3.9 mm., ovigerous females 2.7 and 4.3 mm.

Breeding.—Ovigerous females from Sihuatenejo Bay in November.

Remarks.—Except for a single specimen collected at Tangola-Tangola Bay by the *Velero III*, *Petrolisthes gracilis* has not been known south of the Gulf of California. I suggested (Haig, 1960, p. 81) that the Tangola-Tangola Bay

record might be erroneous. However, the specimens taken by the *Zaca* confirm the presence of the species in southern Mexico.

***Petrolisthes tridentatus* Stimpson**

Petrolisthes tridentatus Stimpson, 1858, p. 227 (*nomen nudum*); 1859, p. 75, pl. 1 fig. 4. Haig, 1960, pp. 29, 81, pl. 25 fig. 4.

Range.—From Salinas Bay, Costa Rica, to Puna Island, Ecuador. Intertidal. Also occurs in western Atlantic.

Material Examined.—18 specimens from 5 stations:

Nicaragua

San Juan del Sur, January 9-12, 1938, intertidal, 1 male, 3 females (12646).

Costa Rica

Port Parker, January 12-23, 1938, intertidal (in coral?), 3 males, 2 females (11834).

Cedro Island, Gulf of Nicoya, February 12-13 or 21-22, 1938, intertidal, 3 males (12647).

Jasper Island, Gulf of Nicoya, February 22-25, 1938, intertidal, 2 males, 3 females (12648).

Ballenas Bay, Gulf of Nicoya, February 25-26, 1938, intertidal, 1 female (12649).

Measurements.—Males 3.9-6.1 mm., nonovigerous females 3.8 and 4.0 mm., ovigerous females 3.6-4.5 mm.

Breeding.—Ovigerous females from San Juan del Sur and Port Parker in January, and from Gulf of Nicoya in February.

Remarks.—One of the specimens from Port Parker was reported by Haig (1960, p. 287). The range of the species is now extended slightly northward from Salinas Bay to San Juan del Sur.

***Petrolisthes galapagensis* Haig**

Petrolisthes galapagensis Haig, 1960, pp. 28, 84, pl. 2, pl. 25 fig. 2.

Range.—Galapagos Islands. Shore to 2½ fathoms.

Material Examined.—Jasper Island, Gulf of Nicoya, Costa Rica, February 22-25, 1938, intertidal, 4 males, 5 females (12650).

Measurements.—Males 4.2-6.3 mm., nonovigerous females 5.0-5.5 mm.

Remarks.—The above record is the first for the species outside the Galapagos Archipelago. In the Galapagos it frequently occurs with its close relative *Petrolisthes tonsorius* Haig, and the two species were encountered together at Jasper Island as well. They are best distinguished by the form of the cheliped: in *P. galapagensis* the margins of the carpus are subparallel, while

in *P. tonsorius* the inner carpal margin is produced into a strong lobe.

***Petrolisthes tonsorius* Haig**

Petrolisthes tonsorius Haig, 1960, pp. 28, 85, pl. 3, pl. 26 fig. 1.

Range.—From Cape San Lucas, Gulf of California, to Santa Elena Point, Ecuador. Revilagigedo, Cocos, and Galapagos Islands. Shore to 10 fathoms.

Material Examined.—36 specimens from 6 stations:

Mexico

Sihuatenejo Bay, November 24, 1937, intertidal under stones, 1 female (12651).

Port Angeles, December 1, 1937, intertidal, 2 males (12652).

Tangola-Tangola Bay, December 8-13, 1937, intertidal, 4 males, 8 females, 2 young (12653).

Nicaragua

Corinto, December 28, 1937-January 7, 1938, intertidal, 1 male (12654).

San Juan del Sur, January 9-12, 1938, intertidal, 1 female (12655).

Costa Rica

Jasper Island, Gulf of Nicoya, February 22-25, 1938, intertidal, 12 males, 5 females (12656).

Measurements.—Males 4.1-9.3 mm., nonovigerous females 3.8-6.2 mm., ovigerous females 3.6-8.3 mm.

Breeding.—Ovigerous females from Sihuatenejo Bay in November, from Tangola-Tangola Bay in December, and from Gulf of Nicoya in February.

***Petrolisthes holotrichus* Nobili**

Petrolisthes holotrichus Nobili, 1901, p. 14. Haig, 1960, pp. 29, 102, pl. 29 fig. 4.

Range.—From Salinas Bay, Costa Rica, to La Libertad, Ecuador. Intertidal.

Material Examined.—4 specimens from 2 stations:

Costa Rica

Ballenas Bay, Gulf of Nicoya, February 25-26, 1938, intertidal, 1 female (12657).

Panama

Bahia Honda, March 13-19, 1938, low tide under stones, 3 females (12658).

Measurements.—Nonovigerous female 2.9 mm., ovigerous females 3.8-5.0 mm.

Breeding.—Ovigerous females from Gulf of Nicoya in February and from Bahia Honda in March.

***Petrolisthes platymerus* Haig**

Petrolisthes platymerus Haig, 1960, pp. 29, 108, pl. 4, pl. 29 fig. 3.

Range.—Known only from Port Parker, Costa Rica, and Taboguilla Island, Panama. Intertidal.

Material Examined.—Ballenas Bay, Gulf of Nicoya, Costa Rica, February 25-26, 1938, intertidal, 1 male (12659).

Measurements.—Male 4.5 mm.

Remarks.—This species was previously known from only 14 specimens collected at two localities. It may have been overlooked by most collectors because of its small size. The largest individual on record is the 5.2 mm. holotype, while egg-bearing females range from 3.5-4.9 mm.

***Petrolisthes ortmanni* Nobili**

Petrolisthes ortmanni Nobili, 1901, p. 16. Haig, 1960, pp. 27, 112, pl. 23 fig. 3.

Range.—From Puerto San Carlos, Gulf of California, to Lobos de Afuera Islands, Peru. Tres Marias Islands and Cocos Island. Shore to 3½ fathoms.

Material Examined.—57 specimens from 7 stations:

Mexico

Tenacatita Bay, November 20, 1937, intertidal, 1 male (12660).

Sihuatenejo Bay, November 24, 1937, intertidal in coral, 2 males, 4 females (12661).

Port Guatulco, December 2-7, 1937, intertidal, 1 female (12662).

Port Guatulco, Station 195, D-15, December 6, 1937, diving in 1½ fathoms, coral, 10 males, 8 females (12663).

Costa Rica

Port Parker, January 12-23, 1938, intertidal (in coral?), 11 males, 13 females (11831).

Jasper Island, Gulf of Nicoya, February 22-25, 1938, intertidal in coral, 3 males, 3 females (12664).

Uvita Bay, March 2-4, 1938, intertidal in coral, 1 male (12665).

Measurements.—Males 2.6-5.6 mm., nonovigerous females 3.2-4.7 mm., ovigerous females 3.6-6.6 mm.

Breeding.—Ovigerous females from Sihuatenejo Bay in November, from Port Guatulco in December, from Port Parker in January, and from Gulf of Nicoya in February.

Remarks.—The specimens from Port Parker were reported earlier by Haig (1960, p. 303).

***Petrolisthes lewisi lewisi* (Glassell)**

Pisosoma lewisi Glassell, 1936, p. 287.

Petrolisthes lewisi Haig, 1957b, p. 7 (not new records nor all of synonymy).

Petrolisthes lewisi lewisi, Haig, 1960, pp. 27, 113, pl. 23 fig. 1.

Range.—From Carmen Island, Gulf of California, to Tequepa Bay, Mexico. Isabel and Tres Marias Islands. Shore to 3 fathoms.

Material Examined.—11 specimens from 3 stations:

Mexico

Sihuatenajo Bay, November 24, 1937, intertidal under stones, 3 females (12666).

Port Guatulco, December 2-7, 1937, intertidal, 2 males, 1 female (12667).

Tangola-Tangola Bay, December 8-13, 1937, intertidal, 4 males, 1 female (12668).

Measurements.—Males 5.0-5.8 mm., nonovigerous females 3.0 and 5.8 mm., ovigerous females 4.3-5.4 mm.

Breeding.—Ovigerous females from Sihuatenajo Bay in November and from Tangola-Tangola Bay in December.

Remarks.—The known range of *Petrolisthes l. lewisi* is now extended southeastward from Tequepa Bay to Tangola-Tangola Bay.

Petrolisthes lewisi austrinus Haig

Petrolisthes lewisi austrinus Haig, 1960, pp. 27, 115, pl. 5, pl. 23 fig. 2.

Range.—From Salinas Bay, Costa Rica, to Santa Elena Point, Ecuador. Intertidal.

Material Examined.—5 specimens from 2 stations:

Nicaragua

Near Potosi River, Gulf of Fonseca, December 23-25, 1937, intertidal, 1 male (12669).

Panama

Bahia Honda, March 13-19, 1938, low tide under stones, 1 male, 3 females (12670).

Measurements.—Males 4.5 and 5.5 mm., nonovigerous females 2.6 and 4.7 mm., ovigerous female 3.3 mm.

Breeding.—Ovigerous female from Bahia Honda in March.

Remarks.—The known range of subspecies *austrinus* is extended northwestward from Salinas Bay to Gulf of Fonseca. The area of contact of the two subspecies of *Petrolisthes lewisi*, which has yet to be determined, lies somewhere between the latter locality and Tangola-Tangola Bay.

Petrolisthes hians Nobili

Petrolisthes hians Nobili, 1901, p. 17. Haig, 1960, pp. 26, 121, pl. 22 fig. 3.

Pisosoma flagraciliata Glassell, 1937, p. 82, pl. 1 fig. 2.

Range.—From Santa Maria Bay, outer Baja California, and Guaymas, Gulf of California, to Santa Elena Bay, Ecuador. Isabel, Tres Marias, and Revillagigedo Islands. Shore to 4 fathoms (exceptionally to 18 fathoms).

Material Examined.—137 specimens from 8 stations:

Mexico

Tenacatita Bay, November 20, 1937, intertidal, 1 male (12671).

Sihuatenajo Bay, November 24, 1937, intertidal in coral, 40 males, 44 females (12672).

Acapulco, November 25-29, 1937, intertidal, 5 males, 4 females (12673).

Port Guatulco, Station 195, D-15, December 6, 1937, diving in 1½ fathoms, coral, 4 males, 2 females (12674).

Costa Rica

Port Parker, January 12-23, 1938, intertidal (in coral?), 7 males, 3 females (11835).

Port Culebra, January 24-31, 1938, intertidal in coral, 4 males, 6 females (12675).

Jasper Island, Gulf of Nicoya, February 22-25, 1938, intertidal in coral, 1 male (12676).

Uvita Bay, March 2-4, 1938, intertidal in coral, 8 males, 8 females (12677).

Measurements.—Males 1.6-5.3 mm., nonovigerous females 2.0-3.9 mm., ovigerous females 1.9-5.1 mm.

Breeding.—Ovigerous females from Sihuatenajo Bay and Acapulco in November, from Port Guatulco in December, from Port Parker and Port Culebra in January, and from Uvita Bay in March.

Remarks.—Two ovigerous females from Sihuatenajo Bay were parasitized by a bopyrid. The specimens from Port Parker were previously reported by Haig (1960, p. 309).

Pisosoma flagraciliata, a synonym of *Petrolisthes hians*, was based on material collected in the Gulf of California during the 1936 Templeton Crocker Expedition.

Neopisosoma mexicanum (Streets)

Pachycheles mexicanus Streets, 1871, p. 225, pl. 2 fig. 1.

Neopisosoma mexicanum, Haig, 1960, pp. 124, 127, pl. 30 fig. 2.

Range.—From Mazatlan, Gulf of California, to Santa Elena Point, Ecuador. Galapagos Islands. Shore to 10 fathoms.

Material Examined.—Corinto, Nicaragua, De-

ember 28, 1937-January 7, 1938, intertidal, 1 female (12678).

Measurements.—Ovigerous female 4.4 mm.

Remarks.—*Neopisosoma dohenyi* Haig, which occupies much the same area as *N. mexicanum* and has been collected with it at Mazatlan and Acapulco, was not taken during the *Zaca* expedition.

***Pachycheles chacei* Haig**

Pachycheles chacei Haig, 1956, pp. 7, 9, pl. 1; 1960, pp. 134, 135, pl. 31 fig. 3.

Range.—From San José, Guatemala, to Santa Elena Bay, Ecuador. 1-4 fathoms. Also Atlantic coast of Panama and Colombia.

Material Examined.—23 specimens from 2 stations:

Costa Rica

Jasper Island, Gulf of Nicoya, February 22-25, 1938, intertidal in coral, 1 male, 2 females (12679).

Uvita Bay, March 2-4, 1938, intertidal in coral, 9 males, 11 females (12680).

Measurements.—Males 2.4-4.7 mm., ovigerous females 2.7-5.2 mm.

Breeding.—Ovigerous females from Gulf of Nicoya in February and from Uvita Bay in March.

Remarks.—The Costa Rican specimens collected by the *Zaca* bridge a considerable gap in the known distribution of the species, which has not been reported previously from the area between Acajutla, El Salvador, and Isla Verde, Panama.

***Pachycheles calculosus* Haig**

Pachycheles calculosus Haig, 1960, pp. 135, 136, pl. 10, pl. 31 fig. 4.

Range.—From Acapulco, Mexico, to La Libertad, Ecuador. Shore to 4 fathoms.

Material Examined.—Sihuatenejo Bay, Mexico, November 24, 1937, intertidal in coral, 2 males (12681).

Measurements.—Males 4.5 and 4.7 mm.

Remarks.—The range of this species is now extended northwestward from Acapulco to Sihuatenejo Bay.

***Pachycheles crassus* (A. Milne Edwards)**

Porcellana (Pachycheles) crassa A. Milne Edwards, 1869, p. 128, pl. 26 fig. 12.

Pachycheles crassus, Haig, 1957b, p. 5; 1960, pp. 134, 141, pl. 31 fig. 1, text-fig. 4.

Range.—From Balboa, Panama, to Gorgona Island, Colombia. Shore to 4 fathoms.

Material Examined.—Sihuatenejo Bay, Mexico, November 24, 1937, intertidal in coral, 2 males, 1 female (12682).

Measurements.—Males 3.9 mm. long, 4.8 mm. wide and 4.8 mm. long, 6.3 mm. wide, ovigerous female 5.6 mm. long, 7.9 mm. wide.

Remarks.—*Pachycheles crassus* was previously known from only nine specimens collected at five localities. The *Zaca* material shows the marked broadening of the carapace, particularly in females, that is characteristic of the species.

The known range is now considerably extended northwestward, from Balboa to Sihuatenejo Bay.

***Pachycheles biocellatus* (Lockington)**

Petrolisthes (Pisosoma) biocellatus Lockington, 1878, pp. 396, 403.

Petrolisthes (Pisosoma) gibbosicarpus Lockington, 1878, pp. 396, 402.

Pisosoma aphrodita Boone, 1932, p. 53, text-figs. 17-18.

Pachycheles biocellatus, Glassell, 1937, p. 84. Haig, 1960, pp. 134, 144, pl. 32 fig. 1. Chace, 1962, p. 619.

Range.—From Espiritu Santo Island, Gulf of California, to La Plata Island, Ecuador. Isabel, Tres Marias, Revillagigedo, Clipperton, and Galapagos Islands. Shore to 13 fathoms.

Material Examined.—112 specimens from 7 stations:

Mexico

Sihuatenejo Bay, November 24, 1937, intertidal in coral, 22 males, 18 females (12683).

Acapulco, November 25-29, 1937, intertidal, 1 male, 1 female (12684).

Port Guatulco, Station 195, D-15, December 6, 1937, diving in 1½ fathoms, coral, 1 male, 1 female (12685).

Costa Rica

Port Parker, January 12-23, 1938, intertidal (in coral?), 16 males, 11 females, 5 young (11830).

Port Culebra, January 24-31, 1938, intertidal in coral, 14 males, 16 females (12686).

Jasper Island, Gulf of Nicoya, February 22-25, 1938, intertidal in coral, 1 male, 3 females (12687).

Uvita Bay, March 2-4, 1938, intertidal in coral, 1 male, 1 female (12688).

Measurements.—Males 2.6-7.0 mm., nonovigerous females 3.0-5.5 mm., ovigerous females 2.8-7.9 mm.

Breeding.—Ovigerous females from Sihuatenejo Bay.

ejo Bay and Acapulco in November, from Port Guatulco in December, from Port Parker and Port Culebra in January, from Gulf of Nicoya in February, and from Uvita Bay in March.

Remarks.—The specimens from Port Parker were recorded earlier by Haig (1960, p. 315). The species was collected in the Gulf of California during the 1936 Templeton Crocker Expedition.

***Pachycheles vicarius* Nobili**

Pachycheles vicarius Nobili, 1901, p. 19. Haig, 1960, pp. 134, 147, pl. 32 fig. 2.

Range.—From Acajutla, El Salvador, to Santa Elena Bay, Ecuador. Shore to 4 fathoms.

Material Examined.—43 specimens from 5 stations:

Costa Rica

Port Parker, January 12-23, 1938, intertidal (in coral?), 7 males, 10 females, 1 young (11832); 1 male, 1 female (AHF).

Port Culebra, January 24-31, 1938, intertidal in coral, 3 males, 3 females (12689).

Jasper Island, Gulf of Nicoya, February 22-25, 1938, intertidal in coral, 1 male, 1 female (12690).

Uvita Bay, March 2-4, 1938, intertidal in coral, 9 males, 5 females (12691).

Panama

Bahia Honda, March 13-19, 1938, intertidal, from *Pocillopora* coral, 1 male (12692).

Measurements.—Males 2.8-6.4 mm., nonovigerous females 3.2-5.2 mm., ovigerous females 3.8-6.2 mm.

Breeding.—Ovigerous females from Port Parker and Port Culebra in January, from Gulf of Nicoya in February, and from Uvita Bay in March.

Remarks.—The Port Parker specimens were recorded and one of them illustrated by Haig (1960, p. 317, pl. 32 fig. 2).

***Pachycheles spinidactylus* Haig**

Pachycheles spinidactylus Haig, 1957a, p. 31, pl. 7 figs. 1-4; 1960, pp. 134, 153, pl. 33 fig. 2.

Range.—From Santa Maria Bay, outer Baja California, and Cape San Lucas, Gulf of California, to Port Utria, Colombia. Isabel Island. Shore to 4 fathoms.

Material Examined.—16 specimens from 3 stations:

Mexico

Sihuatenejo Bay, November 24, 1937, intertidal in coral, 6 males, 7 females (12693).

Costa Rica

Port Culebra, January 24-31, 1938, intertidal in coral, 1 female (12694).

Jasper Island, Gulf of Nicoya, February 22-25, 1938, intertidal in coral, 1 male, 1 female (12695).

Measurements.—Males 4.9-7.9 mm., ovigerous females 3.5-8.4 mm.

Breeding.—Ovigerous females from Sihuatenejo Bay in November, from Port Culebra in January, and from Gulf of Nicoya in February.

***Pachycheles panamensis* Faxon**

Pachycheles panamensis Faxon, 1893, p. 175.

Haig, 1960, pp. 134, 155, pl. 33 fig. 1; 1962, p. 182.

Pachycheles sonorensis Glassell, 1936, p. 291.

Range.—From Tiburon Island, Gulf of California, to Santa Elena Bay, Ecuador. Isabel Island. Shore to 4 fathoms.

Material Examined.—58 specimens from 4 stations:

Mexico

Tenacatita Bay, November 20, 1937, intertidal, 1 male, 1 female (12696).

Sihuatenejo Bay, November 24, 1937, intertidal in coral, 25 males, 27 females, 2 young (12697).

Port Guatulco, Station 195, D-14, December 6, 1937, 4 fathoms, coral, 1 young female (12698).

Costa Rica

Uvita Bay, March 2-4, 1938, intertidal in coral, 1 female (12699).

Measurements.—Males 3.2-8.0 mm., nonovigerous female 9 mm., ovigerous females 3.6-9.1 mm.

Breeding.—Ovigerous females from Tenacatita and Sihuatenejo Bays in November and from Uvita Bay in March.

Remarks.—Material of this species was collected in the Gulf of California during the 1936 Templeton Crocker Expedition and reported by Glassell (1937) as *Pachycheles sonorensis*.

***Pachycheles trichotus* Haig**

Pachycheles trichotus Haig, 1960, pp. 134, 157, pl. 12, pl. 32 fig. 3.

Range.—Known only from Acajutla, El Salvador, and Isla Verde, Panama. Probably intertidal.

Material Examined.—Corinto, Nicaragua, December 28, 1937-January 7, 1938, intertidal, 1 male (12700).

Measurements.—Male 3.8 mm. long, 4.1 mm. wide.

Remarks.—The single specimen collected by the *Zaca* agrees very closely with the only specimens previously known, the male holotype from Isla Verde, Panama, and two ovigerous females from Acajutla, El Salvador. The Corinto male is smaller than the three types, which are nearly identical in size:

Male holotype: 4.7 mm. long, 5.4 mm. wide.

Ovigerous female paratype: 4.7 mm. long, 5.3 mm. wide.

Ovigerous female paratype: 4.8 mm. long, 5.3 mm. wide.

***Minyocerus kirki* Glassell**

Minyocerus kirki Glassell, 1938, p. 430, pl. 31.

Haig, 1960, p. 193, pl. 37 fig. 1, text-fig. 8; 1962, p. 185.

Range.—From Punta Peñasco and San Felipe, Gulf of California, to Realejo, Nicaragua. Shore to 13 fathoms.

Material Examined.—72 specimens from 3 stations:

El Salvador

Cutuco, Gulf of Fonseca, December 21, 1937, 1 male, 3 females (AHF).

La Union, Gulf of Fonseca, Station 199, D-7 to D-16, December 27, 1937, 5-6 fathoms, 12 males, 12 females, 24 young (AHF).

Nicaragua

Monypenny Point, Gulf of Fonseca, Station 199, D-5 and D-6, December 24, 1937, 4-7 fathoms, 9 males, 11 females (AHF).

Measurements.—Males 2.9-3.8 mm., nonovigerous females 3.5-3.7 mm., ovigerous females 3.1-5.5 mm.

Breeding.—Ovigerous females from all three localities in the Gulf of Fonseca.

Remarks.—All the material listed above was reported by Haig (1960, p. 334) and is in the collections of the Allan Hancock Foundation.

Specimens of *Minyocerus kirki* have been reported living as commensals with sea stars, *Luidia columbia* (Gray) and *Luidia phragma* H. L. Clark. Of specimens collected by the *Zaca*, those from Cutuco were "around mouth of sea star" and those from La Union and Monypenny Point "on serpent stars and sea stars." As I have already noted (Haig, 1960, pp. 195 and 196), the sea star was probably *Luidia foliolata* Grube and the serpent star either *Amphipholis platydisca* Nielsen, *Ophiothrix spiculata* Lecomte, or *Ophiolepis grisea* H. L. Clark.

***Porcellana cancrisocialis* Glassell**

Porcellana cancrisocialis Glassell, 1936, p. 292.

Haig, 1960, pp. 198, 200, pl. 38 fig. 2, text-fig. 9(2); 1962, p. 187.

Range.—From Santa Maria Bay and Point Tosco, outer Baja California, and Punta Peñasco, Gulf of California, to Santa Elena Bay, Ecuador. Isabel Island. Shore to 54 fathoms.

Material Examined.—14 specimens from 5 stations:

Mexico

Tenacatita Bay, Station 183, D-2, November 21, 1937, 30 fathoms, muddy sand, 1 male, 1 female (12701).

17 miles southeast by east of Acapulco, Station 189, D-1, November 29, 1937, 20 fathoms, sandy mud, algae, 2 males, 1 female, 1 young (12702).

Port Guatulco, Station 195, D-11, December 6, 1937, 5 fathoms, gray sand, crushed shell, 1 male (12703).

Costa Rica

Port Parker, Station 203, D-2, January 20, 1938, 10 fathoms, shelly sand, algae, 2 females (12704).

Port Culebra, Station 206, D-1, January 30, 1938, 14 fathoms, sandy mud, 2 males, 3 females (12705).

Measurements.—Males 3.7-6.9 mm., nonovigerous females 3.7 and 4.1 mm., ovigerous females 4.5-8.6 mm.

Breeding.—Ovigerous females from Acapulco in November and from Port Parker and Port Culebra in January.

Remarks.—Specimens of this species have frequently been found living in association with hermit crabs, but there is no evidence that this was the case as far as the *Zaca* material is concerned. The species was collected in the Gulf of California by the 1936 Templeton Crocker Expedition (Glassell, 1937).

***Porcellana paguriconviva* Glassell**

Porcellana paguriconviva Glassell, 1936, p. 293.

Haig, 1960, pp. 198, 203, pl. 38 fig. 1, text-fig. 9(3); 1962, p. 185.

Range.—From Magdalena Bay, outer Baja California, and Punta Peñasco, Gulf of California, to Taboga and Taboguilla Islands, Panama. Shore to 50 fathoms.

Material Examined.—9 specimens from 4 stations:

Mexico

Port Guatulco, Station 195, D-2, December 4, 1937, 3 fathoms, sand, 1 male, 1 female (12706).

Costa Rica

Port Parker, Station 203, D-2, January 20, 1938, 10 fathoms, shelly sand, algae, 1 female (12707); D-13, January 22, 1938, 7-9 fathoms, shells, algae, 1 male (12708).

Port Culebra, January 24-31, 1938, intertidal, 2 males, 1 female (12709).

Panama

Bahia Honda, Station 222, D-2, March 18, 1938, 4-8 fathoms, rocks, dead coral, 1 male, 1 young female (12710).

Measurements.—Males 3.2-8.1 mm., nonovigerous female 3.0 mm., ovigerous females 7.3-8.2 mm.

Breeding.—Ovigerous females from Port Guatulco in December and from Port Parker and Port Culebra in January.

Remarks.—According to an accompanying note, the specimens from Port Culebra were found "on body of giant hermit inside shell." The "giant hermit" may have been *Petrochirus californiensis* Bouvier, a large species with which the types of *Porcellana paguriconviva* were associated. However, the identity of the hermit crab cannot be confirmed at this time because the pagurids from the 1937-1938 Zaca Expedition have not been located, according to Jocelyn Crane.

Porcellana paguriconviva was collected in the Gulf of California by the 1936 Templeton Crocker Expedition (Glassell, 1937).

Pisidia magdalenensis (Glassell)

Porcellana magdalenensis Glassell, 1936, p. 295.

Pisidia magdalenensis, Haig, 1960, p. 209, pl. 38 fig. 4, text-fig. 10; 1962, p. 187.

Range.—From Santa Maria Bay, outer Baja California, and Petatlan Bay, Mexico, to Santa Elena Bay, Ecuador. Shore to 25 fathoms.

Material Examined.—87 specimens from 8 stations:

Mexico

Port Guatulco, Station 195, D-2, December 4, 1937, 3 fathoms, sand, 1 male, 2 females (12711); D-11, December 6, 1937, 5 fathoms, gray sand, crushed shell, 1 male (12712); D-16, December 7, 1937, 10 fathoms, sand, 1 male (AHF).

Nicaragua

Corinto, Station 200, D-1, December 29, 1937, 6½ fathoms, mangrove leaves, 1 female (12713); D-6, December 29, 1937, 2½ fathoms, mangrove leaves, 4 males, 1 female (12714); D-14, January 5, 1938, 3 fathoms, mangrove leaves, 1 male, 1 female (AHF); D-

27 to D-30, January 7, 1938, 3 fathoms, 18 males, 23 females (12715).

Costa Rica

Port Parker, Station 203, D-2, January 20, 1938, 10 fathoms, shelly sand, algae, 4 males, 1 female (12716); D-4, January 22, 1938, 7 fathoms, gravel, algae, 1 female (AHF); D-7, January 22, 1938, 9-5 fathoms, shells, algae, 2 males, 2 females (12717); D-13, January 22, 1938, 7-9 fathoms, shells, algae, 2 males, 3 females (12718).

Port Culebra, January 24-31, intertidal in coral, 2 males (12719).

Port Culebra, Station 206, D-1, January 30, 1938, 14 fathoms, sandy mud, 1 female (12720).

Cedro Island, Gulf of Nicoya, Station 213, D-7 and D-9, February 13, 1938, 4-6 fathoms, mud, sand, crushed shell, 4 males, 5 females (12721).

Golfito, Gulf of Dulce, Station 218, D-5, March 9, 1938, 6 fathoms, mangrove leaves, mud, shells, 1 male, 3 females (12722).

Panama

Bahia Honda, Station 222, D-2, March 18, 1938, 4-8 fathoms, rocks, dead coral, 1 male, 1 female (12723).

Measurements.—Males 2.5-4.4 mm., nonovigerous females 2.2-3.0 mm., ovigerous females 2.2-4.0 mm.

Breeding.—Ovigerous females from Port Guatulco in December, from Corinto in late December and early January, from Port Parker and Port Culebra in January, from Gulf of Nicoya in February, and from Gulf of Dulce and Bahia Honda in March.

Remarks.—A portion of the material from Port Guatulco, Corinto, and Port Parker was reported earlier by Haig (1960, pp. 338, 339).

Megalobrachium poeyi (Guérin)

Porcellana poeyi Guérin, 1855, pl. 2 fig. 4.

Megalobrachium poeyi, Benedict, 1901, p. 136, pl. 3 fig. 8. Haig, 1960, pp. 213, 214, pl. 16 fig. 4, pl. 39 fig. 1; 1962, p. 188.

Range.—From Salinas Bay, Costa Rica, to San Francisco near Panama City, Panama. Shore to 25 fathoms. Also occurs in western Atlantic.

Material Examined.—3 specimens from 2 stations:

Costa Rica

Cedro Island, Gulf of Nicoya, February 12-13 or 21-22, 1938, intertidal, 1 male (12724).

Panama

Bahia Honda, March 13-19, 1938, low tide under stones, 1 male, 1 female (12725).

Measurements.—Males 3.5 and 3.7 mm., nonovigerous female 5.9 mm.

Remarks.—Although widely distributed in the Caribbean area, this species appears to be confined to Costa Rica and Panama on the Pacific coast, where only 13 specimens are reported, including the three cited above.

Megalobrachium garthi Haig

Megalobrachium garthi Haig, 1957a, p. 39, pl. 10 figs. 1-5; 1960, pp. 213, 220, pl. 16 fig. 7, pl. 39 fig. 4.

Range.—From Turner Island, Gulf of California, to Port Utria, Colombia. Tres Marias Islands. Shore to 4 fathoms.

Material Examined.—8 specimens from 4 stations:

Mexico

Sihuatenejo Bay, November 24, 1937, intertidal in coral, 3 males, 1 female (12726).

Port Guatulco, Station 195, D-15, December 6, 1937, diving in 1½ fathoms, coral, 2 males (12727).

Costa Rica

Jasper Island, Gulf of Nicoya, February 22-25, 1938, intertidal in coral, 1 female (12728).

Uvita Bay, March 2-4, 1938, intertidal in coral, 1 female (12729).

Measurements.—Males 3.9-6.0 mm., nonovigerous female 2.8 mm., ovigerous females 5.0 and 5.1 mm.

Breeding.—Ovigerous females from Sihuatenejo Bay in November and from Gulf of Nicoya in February.

Remarks.—The specimens from Costa Rica are the first to be reported from the wide geographical area between Tangola-Tangola Bay, Mexico, and Secas Islands, Panama.

Megalobrachium festai (Nobili)

Porcellanides festae Nobili, 1901, p. 21.

Megalobrachium festai, Haig, 1960, pp. 213, 226, pl. 16 fig. 10, pl. 40 fig. 3.

Range.—From Acapulco, Mexico, to Santa Elena Bay, Ecuador. Shore to 4 fathoms.

Material Examined.—Sihuatenejo Bay, Mexico, November 24, 1937, intertidal in coral, 4 males, 4 females (12730).

Measurements.—Males 2.0-3.8 mm., nonovigerous females 3.5-4.3 mm., ovigerous female 2.2 mm.

Remarks.—Until now only 49 specimens of

Megalobrachium festai have been recorded, 41 of which were taken from sponges dredged off Acapulco by the *Velero IV*. Material was collected at three localities in Mexico and one each in El Salvador and Ecuador.

The known range of the species is now extended northwestward from Acapulco to Sihuatenejo Bay.

Megalobrachium tuberculipes (Lockington)

Pachycheles tuberculipes Lockington, 1878, pp. 396, 404.

Megalobrachium tuberculipes, Haig, 1960, pp. 213, 227, pl. 16 fig. 11, pl. 40 fig. 4.

Range.—From Punta Peñasco and San Felipe, Gulf of California, to Santa Elena Bay, Ecuador. Shore to 10 fathoms.

Material Examined.—4 specimens from 2 stations:

Mexico

Sihuatenejo Bay, November 24, 1937, intertidal in coral, 1 male (12731).

Costa Rica

Jasper Island, Gulf of Nicoya, February 22-25, 1938, intertidal in coral, 3 males (12732).

Measurements.—Males 2.6-3.0 mm.

Remarks.—This species seems to be best adapted for concealment in sponges. The specimens collected at Gulf of Nicoya by the *Zaca* Expedition are the first to be recorded between Acapulco, Mexico, and Pearl Islands, Panama.

Polyonyx confinis Haig

Polyonyx confinis Haig, 1960, pp. 233, 234, pl. 17, text-fig. 12(3).

Range.—Known only from Corinto, Nicaragua.

Material Examined.—Corinto, Nicaragua, Station 200, D-14, January 5, 1938, 3 fathoms, mangrove leaves, male holotype (AHF 3817), 1 female paratype (AHF).

Measurements.—Male holotype 2.7 mm. long and 3.6 mm. wide, ovigerous female paratype 2.4 mm. long and 3.6 mm. wide.

Remarks.—This species, which is known only from the two types collected by the *Zaca*, was described by Haig (1960). Both types are housed in the Allan Hancock Foundation.

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6

Observations on the African Bushpig *Potamochoerus porcus* Linn. in Rhodesia

LYLE K. SOWLS¹ AND ROBERT J. PHELPS²

(Plates I-II; Text-figures 1-8)

INTRODUCTION

ALTHOUGH the African bushpig is widely distributed and locally abundant it is one of the continent's least known large mammals. Its elusive habits and the fact that it feeds mostly at night make it better known by its trail of damaged crops than by its appearance. Consequently, except for records on museum specimens which are relatively scarce, very little factual information has been published on this mammal.

This paper is an attempt to bring together most of the existing knowledge of the bushpig and to add new information based largely on experience with animals raised in captivity.

METHODS OF STUDY

In November, 1962, farmers in the Salisbury area of Rhodesia were asked through radio and newspapers to notify us of any young bushpigs found in the area. Seventeen young bushpigs, taken from six litters, were obtained in this way and held in captivity for periods of 13 to 26 months. Of this group all but two survived and flourished. At the beginning these animals were weighed and measured and their teeth examined at weekly intervals. As they became larger they were weighed and measured only once monthly.

¹Arizona Cooperative Wildlife Research Unit, University of Arizona, Tucson, Arizona.

²Agricultural Research Council of Central Africa, Pax House, Salisbury, Rhodesia.

To obtain skulls from pigs of known age the animals were sacrificed at various ages between 13 and 26 months.

Several farmers in the Salisbury, Mazoe, and Concession areas, where there are relatively high bushpig populations, cooperated by gathering weights and measurements of bushpigs killed. One hundred and thirty-seven skulls in the Bulawayo Museum were examined to obtain information on tooth eruption, presence or absence of premolars, and reliability of the extension of the maxilla for sex determination.

FINDINGS

Dentition and Replacement

Normal Dentition.—The total number of teeth for a normal bushpig can vary from 40 to 44 according to the following formula:

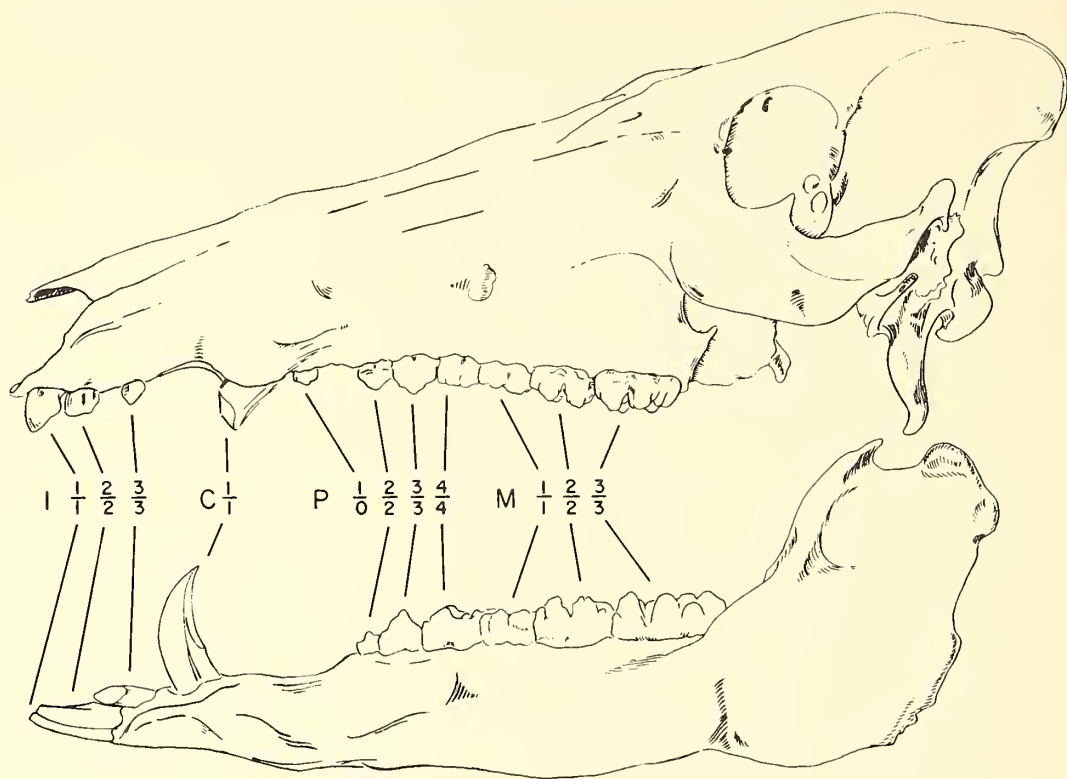
Incisors = $\frac{3}{3}$; Canines $\frac{1}{1}$; Premolars $\frac{3 \text{ or } 4}{3 \text{ or } 4}$;

Molars $\frac{3}{3} \times 2 = 40, 42 \text{ or } 44$

Ninety-two skulls of adults were examined. Of this number, 73, or 79.3 percent, had 42 teeth; 16, or 17.4 percent, had 40 teeth; and only 3, or 3.2 percent, had 44 teeth.

For purposes of our study we numbered the teeth as shown in Text-figure 1. This drawing represents the most common situation where the upper first premolars, but not the lower, are present.

The tusks or canine teeth of the bushpig are



TEXT-FIG. 1. Normal dentition of the African bushpig and system of labeling individual teeth.

not nearly as long and conspicuous as those of the warthog (*Phacochoerus aethiopicus*). The lower canine is generally larger than the upper and is sharpened by wearing action against the upper canine.

Measurements were obtained of both upper and lower tusks of both males and females. Upper tusks of 23 males averaged 20.4 mm. and of 14 females 17.4 mm. These figures were ($t=1.41$ Tab. t. 05 for 35 d. f.=2.03) not significantly different. However, the lower tusks of 29 males which averaged 47.5 mm. in length were found to be significantly longer than 16 lower tusks of females which averaged 41.4 mm. in length ($t=5.79$, Tab. t. 01 for 43 d. f.=2.69).

Order of Eruption and Replacement of Teeth.—At birth the bushpig normally has all four temporary canines and the upper and lower third incisors. The third premolar is the next temporary tooth to erupt in both the upper and lower jaw. The first incisor in both jaws follows at nearly the same time as the fourth temporary premolar. The second premolar follows this. The last temporary tooth to erupt is the second incisor. By 15 to 17 weeks the temporary dentition is complete. At this time the first permanent tooth to erupt is the first lower molar, followed

shortly by the first upper molar. At about 43 to 45 weeks the permanent canines begin to appear. The upper canines appear about two weeks ahead of the lower. The ages at which the various teeth first appeared in the 15 captives are summarized in Table I.

Weights and Measurements

Only meager information on the size of wild bushpigs has been published. A review of the weight and body measurement data found in the literature is summarized in Table II. Table III gives the weights and standard measurements for ten wild bushpigs examined in Rhodesia during 1962 and 1963. The field-dressed weight is that of the head, skin, and body after heart, lungs, and other viscera have been removed.

Growth

No data have been published on the growth rate of wild, free-ranging bushpigs. In 1962 and 1963 we were able to raise 15 bushpigs from a few weeks of age, when they were taken from the nest. Weights and standard measurements were taken at periodic intervals. These animals were given canned milk and water when very young and slowly transferred to a commercial-

TABLE I
TOOTH DEVELOPMENT OF THE AFRICAN BUSHPIG AS DETERMINED
BY PERIODIC EXAMINATIONS OF CAPTIVE ANIMALS

	Temporary Teeth			Permanent Teeth		
	(Age at Tooth Eruption in Weeks)			(Age at Tooth Eruption in Weeks)		
	No. Animals	Range	Mean	No. Animals	Range	Mean
<i>Upper Jaw</i>						
Incisors, 1st	9	7-9	7.7	2	71-75	73.0
2nd	10	11-17	13.8	1	95	...
3rd	In at birth					
Canines	In at birth			12	36-49	43.6
Premolars, 1st	No temporary tooth			13	30-41	33.1
2nd	12	9-15	11.8	3	71-78	74.4
3rd	9	4-6	5.0	3		
4th	9	8-12	9.8	3		
Molars, 1st	No temporary tooth			13	21-26	24.5
2nd	No temporary tooth			5	56-68	61.0
3rd	No temporary tooth					
<i>Lower Jaw</i>						
Incisors, 1st	9	3-7	5.5	2	72-75	73.5
2nd	10	9-14	10.8	1	88	...
3rd	In at birth					
Canines	In at birth			10	45-53	47.8
Premolars, 1st	No temporary tooth			none	?	?
2nd	7	11-16	12.8	3	71-78	74.4
3rd	9	4-6	5.0	3		
4th	8	8-12	9.6	3		
Molars, 1st	No temporary tooth			14	20-26	22.8
2nd	No temporary tooth			4	56-68	63.0
3rd	No temporary tooth					

TABLE II
WEIGHTS AND BODY MEASUREMENTS OF BUSHPIGS AS DESCRIBED IN THE LITERATURE

<i>Area of Collection</i>	<i>Approx. Age</i>	<i>Sex</i>	<i>Weight (lbs.)</i>	<i>Head & Body</i>	<i>Shoulder Height</i>	<i>Hind Foot</i>	<i>Ear</i>	<i>Tail</i>	<i>Reference</i>
S. Africa	Adult	M	...	50.5	...	10.5	6.0	14.7	Shortridge (1934)
Kenya		M	...	51.0	...	10.5	5.5	14.0	
Zambia		F	171	47.4	25.5	10.2	6.8	15.5	Ansell (collector), Bulawayo Museum
S. Africa		M	...	51.1	...	8.9	...	12.4	Roberts (1951)
		M	250		Shortridge (1934)
		F	200		
	235						Shortridge 1934 from Kirby
Zambia	...	M	175			Robinette (1963) from Ansell
	...	F	135						
	...	F	122						Robinette (1963) from Benson

type hog feed given twice daily. Text-figure 2 shows the rate of gain of males and Text-figure 3 gives the rate of gain of the females. An approximate rate of growth is represented by the curved line which has been drawn by inspection.

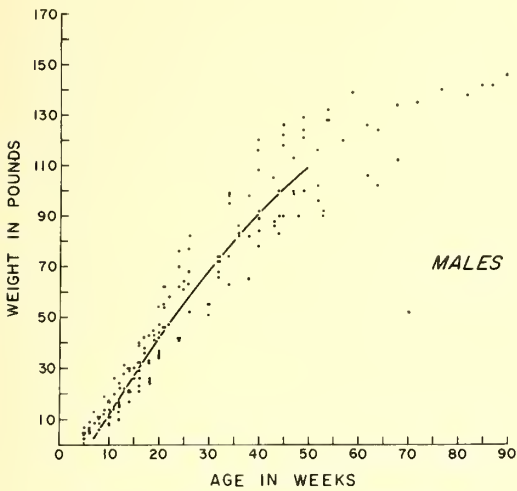
When they were first obtained animals were kept in small pens about ten feet square, at a rate of four or five animals per pen.

At about four months of age all 15 bushpigs were placed in one large pen with a total area of about 900 square feet, of which about 30 percent was sheltered.

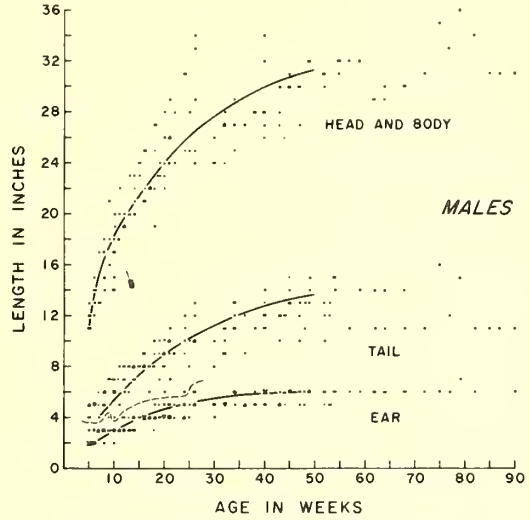
Growth curves were not plotted beyond the 50-week mark. Several factors made the data after this age less reliable. As the animals were sacrificed the number of values obtained for the

TABLE III
WEIGHTS AND BODY MEASUREMENTS OF WILD BUSHPIGS FROM RHODESIA

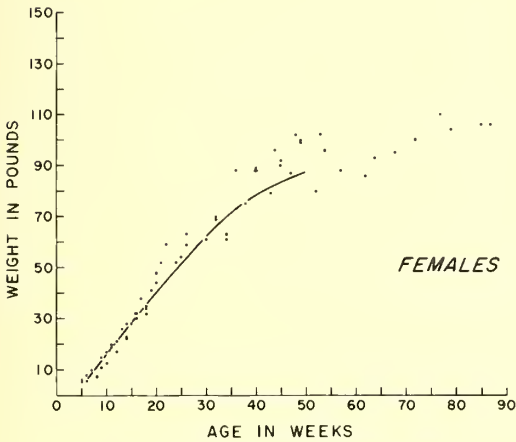
Area of Collection	Approx. Age	Sex	Weight (lbs)	Field-dressed Weight (lbs)	% Loss	Measurement in Inches					Collector or Measurer
						Head & Body	Shoulder Height	Hind Foot	Ear	Tail	
Concession, Rhodesia	Adult	F	155	114	26	47	27	10	6.75	12	Durand (collector)
	F	106	85	20	46	26.5	10.5	...	6.75	Peak (collector)
	Adult	M	157	125	20	52	30.25	11.5	7.5	14	Maratos (measurer)
	F	116	90	24	45		10	5	14	
	3-4 mos.	F	22	17	23	25	14	6	3.75	7.5	
	Adult	M	144	118	18	51	31	11	7	17	
Near Salisbury, Rhodesia	Imm. about 1 yr.	F	98	76	24	36	24	10	5.25	14	Sowls (measurer)
		M	101	81	20	38	23	10	5.5	14	
	Adult	M	183	149	19	48	29	10.5	6.25	...	



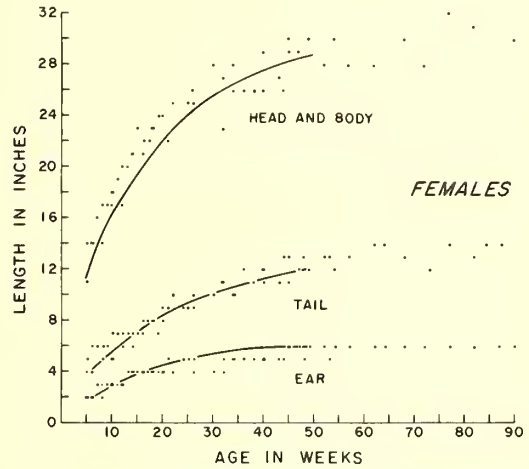
TEXT-FIG. 2. Rate of gain in weight of captive male bushpigs.



TEXT-FIG. 4. Rate of increase of head and body length, tail length, and ear length in captive male bushpigs.



TEXT-FIG. 3. Rate of gain in weight of captive female bushpigs.



TEXT-FIG. 5. Rate of increase of head and body length, tail length, and ear length in captive female bushpigs.

various ages became fewer and fewer; of the 15 animals obtained only four were females; the effects of the experimentation with trypanosomiasis were not known. Although the bushpig is a highly social animal and individuals appeared to be compatible, unequal gain in weight and general growth were probably caused by crowding, especially when the animals were over one year of age.

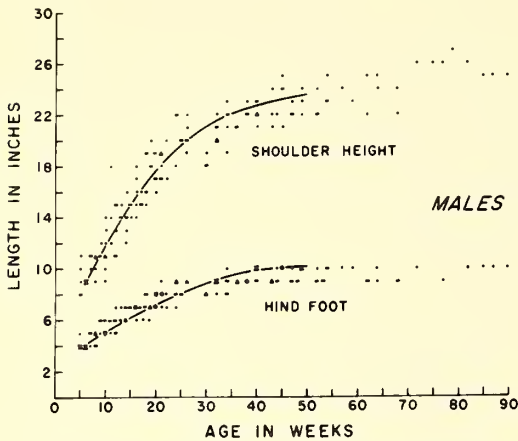
Text-figures 4 and 5 show the rate of increase in length of ear, tail, and length of head and body and Text-figures 6 and 7 give the rate of increase in hind foot length and shoulder height.

Both sexes showed a rather uniform rate of

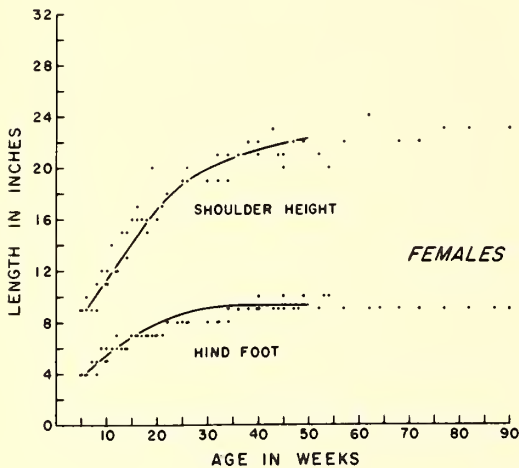
growth during the first year of life and gained weight at the rate of about two pounds per week.

Some indication of the meaning of the growth rates can be obtained by comparing them with the weights and measurements of wild animals. Old adults (Tables II and III) have been found to vary in weight by about 40 pounds. Two wild animals determined to be yearlings by the tooth eruption pattern weighed nearly the same as captive animals at the age of one year.

The increase in head and body measurements formed a steep curve until about 40 weeks. Com-



TEXT-FIG. 6. Rate of increase of height of shoulder and length of hind foot in captive male bushpigs.



TEXT-FIG. 7. Rate of increase of height of shoulder and length of hind foot in captive female bushpigs.

parisons with the figures on wild animals indicate that this measurement continues until much later in life than the 90 weeks which is represented by the oldest animals in Text-figures 4 and 5.

Shoulder height in both sexes began to decline in rate of increase among captive animals at about 30 weeks, and like the length of head and body did not show a definite flat curve at the 90 weeks at which the oldest animals were sacrificed in these investigations. Like the length of head and body the height at shoulder continues to increase slightly after 90 weeks.

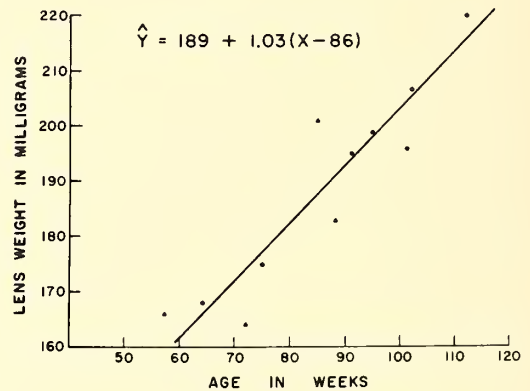
The length of hind foot and ear were the earliest to show a leveling off of the curve among

the captive animals and showed the least variation of all measurements.

The length of the tail among wild specimens was found to vary by about 30 percent. The flattening of the curve at about 50 weeks for the small number of captive individuals on which data were obtained apparently means that these particular individuals had already reached adult tail length.

Lens Weight as an Index to Age.—Among the Suidae and related forms, lens weight as an index to age has been studied in the warthog *Phacochoerus aethiopicus* by Child, Sowls, and Richardson (1965) and the collared peccary *Pecari tajacu* by Richardson (1966).

Data on the lens weights of the bushpig are scarce. However, we are showing the weight-age relationship for the 12 sets of lenses from the captive bushpigs in Text-figure 8. The lens weight plotted is the average for the two lenses which were oven-dried and weighed to the nearest milligram.



TEXT-FIG. 8. Lens weight-age relationship in 11 specimens of bushpig.

Determining Sex from the Skull.—The male bushpigs can be distinguished from the female by a dorsal extension of the maxilla which extends from the base of the canine (Pl. I, Figs. 1 & 2). This process has been described by Roberts (1951), Shortridge (1934), and other writers. Of the 92 adult skulls examined in this study the record described all skulls with the process as males and all without it as females except one, which we suspect was incorrectly labeled.

Reproduction

Breeding Season and Litter Size.—Only meager information on reproduction in bushpigs ap-

pears in the literature. Asdell (1964) gives the gestation period as four months. Phillips (1926) says that in South Africa there is no definite breeding season and that litters generally number four. Fitzsimmons (1920), however, gives midsummer (December and January) as the period of parturition in South Africa. Shortridge (1934) quotes Kirby, who gave the same period and says litters are made up of five to six young. In Zambia, Ansell (1960a) says that records of recently born young are from October to March and that the litter sizes range from two to six with three to four the most common.

Among the specimens of bushpigs in the collection of the National Museum of Rhodesia at Bulawayo are 14 very young animals as follows: three from the same litter taken in Zambia on December 21, 1959, which were apparently collected when only a few weeks old; two from one litter collected by W. F. H. Ansell on February 10, 1950; three from one litter collected by B. O. Williams from Turk Mine in Rhodesia in July 1960, which according to the tooth pattern and measurements had apparently been born in March; three collected together at Nagupande, Rhodesia, on November 25, 1962; one collected near Salisbury on January 7, 1963, which was estimated to be about two weeks old; one from Zambia collected on January 25, 1961; and one collected by W. F. H. Ansell on March 30, 1956.

The records on time of parturition and litter

size obtained in this study are given in Table IV. Most of the farmers to whom we talked in the Mazoe-Salisbury-Concession area believed that most of the young bushpigs in that area were born between late November and about February 1. We conclude that in Rhodesia the principal parturition season is the same as Ansell has described for Zambia with the largest number of animals being born in November, December, and January. This period is during the summer rainy season when the food supplies and the young animals' chances for survival would be the best. This same type of timing of the parturition season and rainfall has been described by Sowls (1964) for another swinelike animal, the collared peccary.

One female in the captive herd gave birth to three young on November 30, 1964, at the age of 103 weeks. The mating in this instance, based on the four-month gestation period, would have occurred about August 1. At this time the sow was 86 weeks old.

The sow makes a large nest of grass for the young. These nests remain for many months in the heavy woodland and resemble a small weathered haystack. Most of the young that were captured for us were taken from the nests by African farm hands. Ansell refers to these nests as bowers.

Table V gives the weight and measurements of five young from two litters that were obtained

TABLE IV
BIRTH DATES AND LITTER SIZE FOR INDIVIDUAL LITTERS

Locality	Date of Birth	Litter Size	Reference or Observer
Concession, Rhodesia	11-23-62	7	Keats
Mazoe, Rhodesia	11-23-62	?	Wheeler
	12-2-62	4+	Edwards
	12-10-62	4+	Bothma
	1-9-63	?	Douglas

TABLE V
WEIGHT AND MEASUREMENTS FOR NEWLY BORN BUSHPIGS

Date	Sex	Est. Age in Days	Weight (Grams)	Flesh measurements mm.				
				Head & Body	Hind Foot	Shoulder Ht.	Tail	Ear
11-27-62	F	4 days	710	260	78	178	94	45
	M		880	260	74	174	96	51
12-6-62	M		877	242	72	162	102	46
	F		849	232	72	165	99	50
	M		679	230	67	148	90	40

by us when about four days old. At birth the young have longitudinal yellowish or white stripes on a brown background (see Pl. II, Fig. 3). The color of individual litters varies considerably. Some pigs are much darker than others and have less distinct stripes. The stripes slowly disappear as the animals grow and the coat becomes reddish. Little evidence of stripes remains after 24 weeks of age.

Behavior

No detailed studies on the behavior of the bushpig have been made. Roberts (1951), Shortridge (1934), Phillips (1926), Ansell (1960b), and other writers all describe the bushpig as a gregarious animal. The herd size has been described by various writers as containing from four to 20 pigs.

Unlike the warthog, which is strictly diurnal, the bushpigs feed almost entirely at night. During the daytime they seek refuge in the tall grass and brush where they remain until darkness. Ansell (1960b) says, however, that in remote country they commonly move about in the daylight when undisturbed.

In captivity young bushpigs become extremely tame but tend to become dangerous as they reach maturity. Among the captives which we raised we found that injured animals were persecuted by their pen mates; the injured pigs had to be separated from the others when cuts or open sores appeared on their bodies.

Bushpigs and Trypanosomiasis

No detailed information is available on the species of trypanosomes that may be carried by bushpigs. Some of the animals kept in the current study were infected with a trypanosome, fatal to domestic pigs, by inoculation of blood from a heavily infected domestic pig. Not all the bushpigs became positive for trypanosomes and those that did apparently were not affected seriously. The trypanosomes could no longer be detected in blood smears taken a few weeks after initial infection. This information was given to the authors in a personal communication from P. McKenzie.

Bushpigs infected with trypanosomes, even if only for a short time, act as carriers of the disease, and the frequency with which they are fed on by tsetse flies determines the importance of the animals in the epidemiology of trypanosomiasis. In Rhodesia, *Glossina morsitans orientalis* Vanderplank and *Glossina pallidipes* Aust are the major tsetse species. *G. morsitans orientalis* falls into the group feeding mainly on suids and bovids (Weitz, 1962), based on information derived from identification of blood meals obtained

from flies in the field. Available information indicates that suids provide 36.1 percent of the meals of *G. morsitans orientalis*, and of the total suid blood meals 14 percent are from the bushpig (Weitz, 1962). *G. pallidipes* falls into the group classed as feeders mainly on bovids (Weitz, 1962). Suid meals comprise 29.9 percent of the total meals taken by this fly, and of the suid meals 41 percent are from the bushpig (Weitz, 1962). The importance of bushpigs in the diet of tsetse in Rhodesia is established by this data, and in other parts of Africa there are tsetse species which are more partial to bushpig blood.

All the tsetse infested country in Rhodesia falls in the range of distribution of the bushpig (Smithers, 1966), and the ranges of the two major tsetse species are almost identical. Control of tsetse by elimination of preferred host species is attempted in some areas of Rhodesia, and bushpigs are one of the animals hunted.

In January, 1965, and April, 1964, four of the captive animals were used for experimental work with trypanosomiasis. Blood samples from bushpigs inoculated with trypanosomes revealed short periods of infection from which the animals recovered, and weight curves did not appear to be affected by the treatment. Further details on this phase of study will be reported by Phelps and Roth.

Food Habits

No detailed study of the foods taken by the bushpig has been made. Fitzsimmons (1920) says that in South Africa they take roots, bulbs, and fruits. Shortridge (1934) agrees but adds that they devour reptiles, eggs, and birds and tells of one instance where the carcass of a bushbuck was eaten by bushpigs. Roberts (1951) says that the normal diet of the bushpig is roots and edible vegetable matter. Phillips (1926) gives a rather extensive list of plants eaten by bushpigs in South Africa. He lists seven species of ferns, nine species of monocotyledons, eight species of dicotyledons, and 26 species under forest tree fruits.

In agricultural areas surrounded by brushy timber the bushpig makes domestic crops a large part of his diet. Maize, groundnuts, and field peas are heavily taken by bushpigs in Rhodesia as the fruits become mature.

Control of Bushpigs

Because of their fondness for agricultural crops they are classed as a major pest in the maize growing area of Rhodesia. In these areas farmers find it necessary to control the bushpig by whatever means possible. The animals destroy far

more of the crop than they can eat (Roberts, 1951), and being largely nocturnal in habit, they are not easy to hunt by conventional methods. The most successful method of hunting the animals is the use of dogs to track them to their lairs which are generally in dense thickets. Even when located, the bushpig is not easy to kill, and can be a formidable adversary. Shotguns are the most useful weapon in hunting the animals, the range at which shooting is done being only a matter of yards. Trapping has not been found to be very effective against bushpigs (Roberts, 1951), and once a trap has been located the animals will make wide detours around it. Bushpigs will sometimes eat carrion (Smithers, 1966) and large animal carcasses are sometimes poisoned in areas infested with bushpigs. The animals may occur very close to settled areas, provided some thick cover remains in gullies or on hill slopes. In such areas enough manpower may be available to organize drives, and this method of hunting sometimes achieves a degree of success.

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EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. Frontal portion of female bushpig skull.
FIG. 2. Frontal portion of male bushpig skull
showing upward extension of maxilla.

PLATE II

- FIG. 3. Young bushpigs two days old.
FIG. 4. Adult male captive bushpig.



FIG. 1



FIG. 2

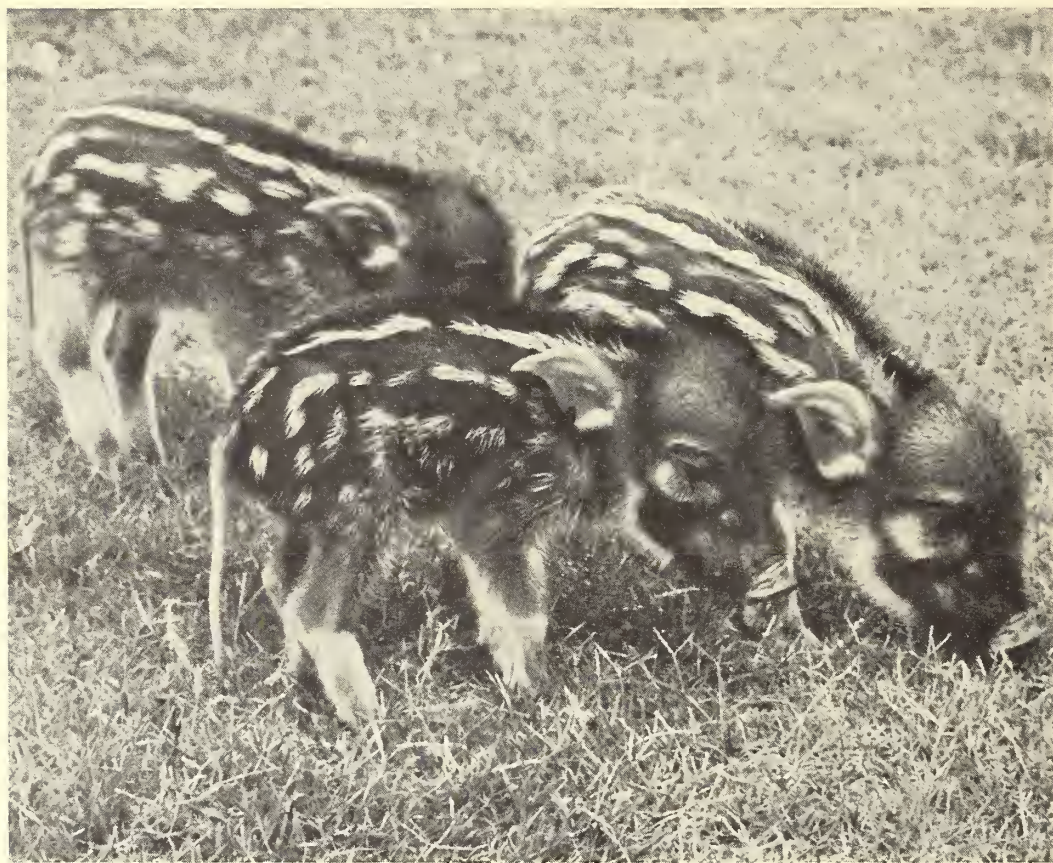


FIG. 4

OBSERVATIONS ON THE AFRICAN BUSHPIG *POTAMOCHOERUS PORCUS* LINN. IN RHODESIA

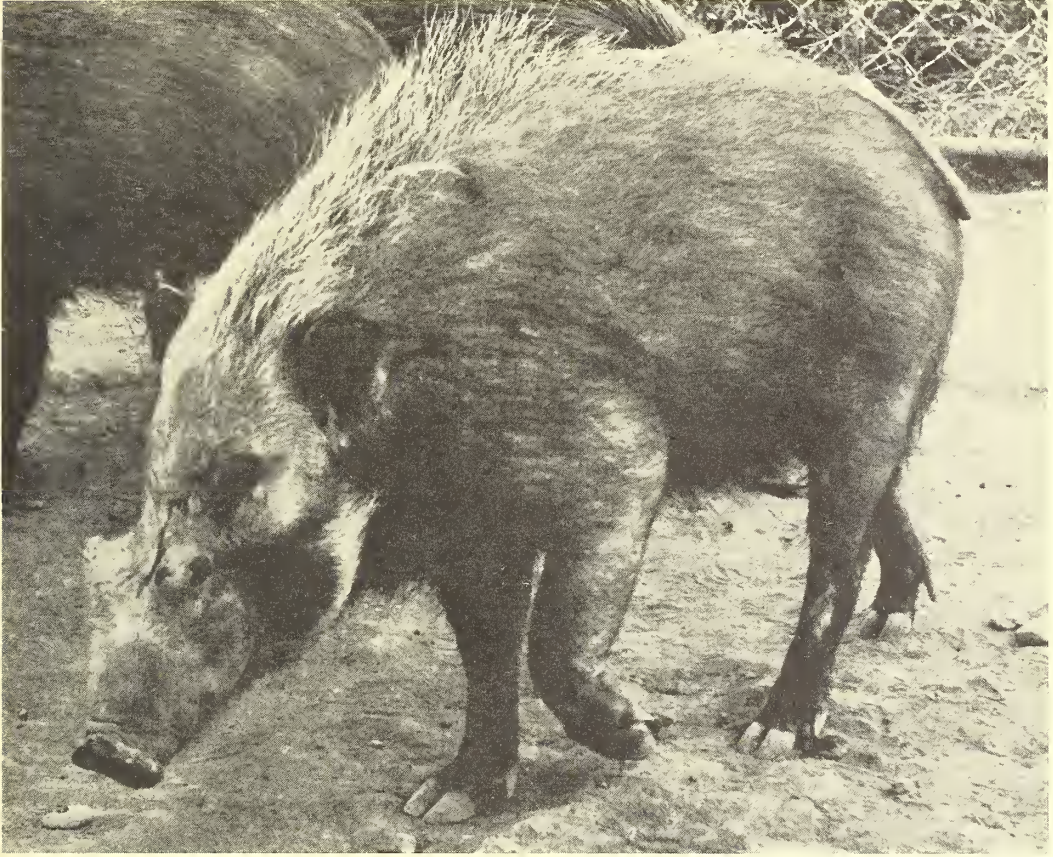


FIG. 3

OBSERVATIONS ON THE AFRICAN BUSHPIG *POTAMOCHOERUS PORCUS* LINN. IN RHODESIA

The Breeding Biology of the Male Brown Bear (*Ursus arctos*)^{1,2}

ALBERT W. ERICKSON,³ HARLAND W. MOSSMAN,³ RICHARD J. HENSEL,⁴ AND WILLARD A. TROYER⁴

(Plates I-IX; Text-figures 1-2)

INTRODUCTION

THE BREEDING BIOLOGY of the brown bear is known in only a general way. Breeding occurs in the spring, usually in late May or June, and its timing does not appear to vary significantly between wild or captive animals or throughout the wide expanse of the species distribution (Dathe, '61; Dittrich and Einsiedel, '61; DeVoto, '53; and Murie, '44). The female exhibits a period of heat extending up to two weeks and is polygamous. During this time coital activity is recurrent but is interrupted by days of nonbreeding (Dittrich and Kronberger, '63).

The age of puberty is unknown in the male bear, but among female captives is usually attained at three and a half years. The gestation period in captivity has been reported as varying between 194 and 278 days (Dittrich and Kronberger, '63). Despite this disparity, a large body of evidence shows whelping to occur regularly in late January and early February regardless

of when breeding occurs. Explanation for this is that bears of the genus *Ursus* have a delayed implantation wherein the fertilized eggs develop to the blastocyst stage and lie quiescent in the uteri for a long period of time. Implantation occurs about the same time in all specimens regardless of when breeding occurs (Wimsatt, '63; and Dittrich and Kronberger, '63). Normally the delays last slightly over half of the gestation period and macroscopic embryos are not visible until about the time of winter denning. The cubs are born in an immature state during the so-called hibernation period. Litters vary from one to four cubs but are usually two or three.

Beyond breeding observations, the only specific information known to us on the reproductive biology of the male bear is a report by Dittrich and Kronberger ('63) on the histology of the testes and epididymides of two captive bears killed in August and October, respectively. On the basis of spermatogenic activity and epididymal sperm observed in both animals, they concluded that male brown bears retain reproductive capability at least through October.

METHODS AND PROCEDURES

The testes, epididymides, and vasa deferentia of 127 brown bears were collected in Alaska between May 20, 1961, and November 11, 1964. The majority of the specimens were from Kodiak Island, but specimens were obtained also from other areas of the state, particularly from the Alaska Peninsula (Table I). Most of the bears were killed by sport hunters. Additional specimens were obtained from bears killed as nuisances or by unilateral castrations of live-trapped bears.

¹Reference to the brown bear here refers collectively to the various so-called species of North American brown and grizzly bears, and to the European and Eurasian brown bears. Recent taxonomic reviews conclude that all of these are simply subforms of *Ursus arctos* L. (Pocock, '32; Erdbrink, '53; Couturier, '54; and Rausch, '62).

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³Anatomy Department, University of Wisconsin Medical School, Madison 53706. Dr. Erickson's present address is James Ford Bell Museum of Natural History, University of Minnesota, Minneapolis 55455.

⁴Kodiak National Wildlife Refuge, Kodiak, Alaska 99615. Mr. Troyer's present address is Kenai National Wildlife Refuge, U.S. Fish and Wildlife Service, Kenai, Alaska.

TABLE I

RESULTS OF EXAMINATIONS OF TESTES, EPIDIDYMIDES,

Location	Specimen Number	Date	Skull ¹ Meas.	Age ² (Years)	Testis ³ Wt. (Gms.)	Testis Tubules	
						Diam. (μ)	Activity ⁴ State
Kodiak Is.	14N	4-7-64	19¼	1.2e	9.7*	NF, G
	36M	5-4-62		18.2	95	NF, G
	12M	5-7-62	19⅝	2.3e	17.2	113	NF, G
	8N	5-8-64	20⅜	2.3a	11.8	NF, G
	47M	5-11-63	22½	2.3e	15.0*	NF, G
	49M	5-13-62	21½	2.3e	19.0*	NF, G
	5M	5-14-62		24.0	112	NF, G
	57M	5-19-63	19½	1.3e	11.0	NF, G
	26M	5-19-62	20½	2.3e	19.4	95	NF, G
	43N	5-19-64	21¼	2.3e	16.7*	NF, G
	K44	5-20-62	2.3a	6.3*	86	NF, G
	65M	5-21-63	19⅞	1.3e	10.0*	NF, G
	E306	7-14-63		11.0*	83	NF, G
	40N	10-7-64		15.0*	81	NF, G
	49N	10-7-64		10.2*	NF, G
Anchorage Kodiak Is.	71M	10-8-63	21⅞	2.7e	10.2*	NF, G
	2M	10-10-62	20⅝	2.7e	16.0	75	NF, G
	3M	10-10-62	20⅝	2.7e	13.9	94	NF, G
	31A	10-11-61	23⅜ ₁₆	2.7a	20.1	NF, G
	4M	10-12-62		21.9	118	NF, G
	67A	10-12-63	20⅜ ₁₆		11.7	81	NF, G
	32A	10-17-61	23⅜ ₁₆	2.8a	19.2	NF, G
	K97	10-17-63	21¼	2.8a	16.5*	NF, G
	34MK	10-19-61		22.9	NF, G
	75M	10-19-63		24.2*	NF, G
	47N	10-22-64	20	2.8e	23.1*	109	NF, G
	20M	10-25-62		15.8	123	NF, G
	52N	10-29-64	2.8e	20.8*	97	NF, G
	18M	10-31-62	21⅞	2.9e	16.3	114	NF, G
	46N	11-2-64	19.0	1.9e	6.5*	54	NF, G
	50N	11-2-64	23½	2.8k	15.8*	NF, G
	51N	11-3-64	20	2.9e	13.2*	96	NF, G
	8M	11-5-62	22½	2.9e	22.1	NF, G
	10M	11-8-62	20⅞	2.9e	15.1	NF, G

^a For explanation of number designations see Table II.

TABLE II

RESULTS OF EXAMINATIONS OF TESTES, EPIDIDYMIDES,

Location	Specimen Number	Date	Skull ¹ Meas.	Age ² Yrs.: Months	Testis ³ Wt. (Gms.)	Testis Tubules		
						Diam. (μ)	Height of Epithel (μ)	Activity ⁴ State
Kodiak Is.	36N	5-7-64		42.5*	SN
	59M	5-11-63		36.0*	S, G
	13N	5-18-64	21⅞	3.3e	33.4	124	NF, G
	21M	5-22-62	22	3.3e	25.6	196	35	SN
	56M	5-24-63		43.0*	173	39	FS, A
Paxson Kodiak Is.	E042	5-25-61		24.5	30.8	187	S, G
	E258	9-16-62		20.0	18.8	123	NF, G
	62A	10-4-62	22⅞ ₁₆	3.9e	31.9*	154	51	SN, G
	32N	10-5-64	22⅜ ₁₆	3.9e	46.0	A, FS
	30N	10-7-64	24⅞	4.9e	34.6*	SN, G
	72M	10-9-63	24	4.9e	27.3	NF, G
	9M	10-10-62		33.9	180	38	SN, G
	73M	10-14-63		29.1	125	57	S, G
	74M	10-17-63	25¼	4.9e	21.4	NF, G

Legend for Tables I, II, III

¹ Skull measurements: Length (occipital protuberance to margin of incisor) + width (outer edges of zygomatic arches).

² Age: k = known age marked animal; a = approximate known age marked animal; e = estimated age.

³ Testis weight: testis + epididymis + vas deferens. The weights marked with an asterisk are preserved weights plus 10% (the mean weight loss between fresh and preserved specimens).

⁴ Spermatogenic activity: FS = free sperm; SN = sperm nuclei or heads in Sertoli cells; S = primary or secondary spermatocytes; A = abnormal forms shed into lumen; G = Edematous (giant) cells in germinal epithelium or in lumen. NF = No formed elements other than giant cells.

AND VASA DEFERENTIA OF INFANTILE BROWN BEARS^a

Intertubular Area			Epididymis					Vas Deferens		
General ⁵ Character	Cytoplasmic		Diam. (μ)	Height of Epithel (μ)	Lumen ⁸ Contents	Coagulum ⁹	Cytoplasmic ¹⁰ Droplets	Lumen ⁸ Contents	Coagulum ⁹	Cytoplasmic ¹⁰ Droplets
	Abundance ⁶	Vacuolation ⁷								
FI	E	+++	E	++	+++
IF	+	A, H	178	48	E	+	+	E	N	+
IF	+	A, H	196	50	E	+	+	E	++	++
FI	+	A, H	150	47	E	+++	+	E	++	++
FI	+	A, H	E	+	++	E	+	++
IF	+	A, H	E	+	+	E	+	+
IF	++	A, H	271	62	E	++	++	E	+	++
FI	+	N
FI	+	A, H	123	36	E	+++	N	E
FI	+	A, H	E	+	+	E	+	++
FI	+	N	169	60	E	++	+	E
FI	+	N	E	E
FI	+	A, H	E	N	+	E
FI	+	A, H	176	51	E	N	N	E	N	N
FI	+	N	E	E
FI	+	N	E	E
I	+	A, H	180	46	E	+	N
FI	+	N	194	57	E	+	+	E	N	+
FI	+	A, H	E	N	N	E	++	++
IF	+	A, H	205	51	E	N	N	E	N	+
IF	+	A, H	206	E	++	N	E	+	N
IF	++	A, H	E	E
IF	++	A, H	E	E
IF	+	A, H	E	E
.....
FI	+	A, H	159	55	E, A	+	+
IF	+	A, H	215	E	++	+	E, D	N	N
IF	+	A, H	122	33	A	+++	+
FI	+	A, H	173	37	E	N	+	E	N	+
FI	++	A, H	150	35	E	++	+
IF	+	A, H	E	+	+	E	N	N
IF	+	A, H	206	E	++	N	E	++	N
FI	+	A, H	E, D	N	+
FI	+	A, H	E, D	N	N

AND VASA DEFERENTIA OF PREPUBERAL BROWN BEARS

Intertubular Area			Epididymis					Vas Deferens		
General ⁵ Character	Cytoplasmic		Diam. (μ)	Height of Epithel (μ)	Lumen ⁸ Contents	Coagulum ⁹	Cytoplasmic ¹⁰ Droplets	Lumen ⁸ Contents	Coagulum ⁹	Cytoplasmic ¹⁰ Droplets
	Abundance ⁶	Vacuolation ⁷								
.....	E	E
I	+	A, H	A, S	+++	+	E, A, S	+	++
IF	+	A, H	E, A	++	N	E	++	+
FI	+	A, H	182	45	A	+	N	A	+	++
I	++	A, H	224	68	S, A	+++	++	S, A	++	N
IF	+	A, H	194	A
FI	+	A, H
IF	+	A, H	224	57	E	+	+	E	N	+
IF	+	A, H	A, S	A, S	N	N
FI	+	L	159	47	A	+	+	A	N	+
IF	+	A, H	E	E
FI	+	L	248	66	E, A	++	+	E, A	+	N
IF	++	A, H	167	E	+	++	E, D	N	N
IF	A, H

⁵ General character of intertubular tissue: FI = more fibrous tissue than interstitial tissue; IF = more interstitial tissue than fibrous tissue; I = predominantly interstitial tissue.

⁶ Leydig cell cytoplasmic abundance: + = low; ++ = med.; +++ = high.

⁷ Leydig cell vacuolation: N = little or none; A = abundant small vacuoles; L = large and small vacuoles; H = vacuoles highly vesicular (frothy).

⁸ Lumen contents: S = apparently viable sperm; A = immature and abnormal forms; D = degradation products of tract; E = empty; several entries indicate differences between ducts in order of decreasing occurrence.

⁹ Prevalence of coagulum in epididymis and vas deferens: N = little or none; + = low; ++ = medium; +++ = abundant.

¹⁰ Cytoplasmic extrusions of epididymis and vas deferens: N = little or none; + = low; ++ = medium; +++ = abundant.

TABLE III

RESULTS OF EXAMINATIONS OF TESTES, EPIDIDYMIDES,

Location	Specimen Number	Date	Skull ¹ Meas.	Testis ³ Wt. (Gms.)	Testis Tubules		Activity ⁴ State
					Diam. (μ)	Height of Epithel (μ)	
Kodiak Is.	41M	4-2-63	29	94*	285	95	FS
	42M	4-18-63	26 $\frac{3}{4}$	83*	271	solid	FS
	22M	4-22-62	23 $\frac{3}{8}$	49	187	solid	FS
	42N	4-28-64	25 $\frac{3}{8}$	58*	FS
	34N	5-1-64	60*	FS
	44M	5-2-63	90*	FS
	16M	5-4-62	28 $\frac{1}{2}$	98	276	76	FS
	45M	5-4-63	28 $\frac{1}{2}$	47*	FS
	1M	5-4-62	28 $\frac{3}{8}$	95	262	95	FS
	33N	5-5-64	28 $\frac{3}{16}$	85*	FS
	43M	5-5-63	28 $\frac{1}{2}$	84*	FS
	31N	5-6-64	27 $\frac{1}{2}$	110*	FS
	13M	5-7-62	26 $\frac{3}{4}$	77	209	57	FS
	31M	5-8-62	89	257	76	FS
	46M	5-9-63	26 $\frac{1}{2}$	46*	FS
	28M	5-10-63	79	FS
	33M	5-10-62	27 $\frac{3}{4}$	97	259	83	FS
Alaska Pen.	E231	5-10-62	72	74	FS, A
Kodiak Is.	61M	5-11-63	28 $\frac{1}{2}$	86*	FS
Alaska Pen.	E305	5-11-64	92	90	FS, A
	1396	5-12-64	76*	80*	266	59
Kodiak Is.	7M	5-13-62	76	268	76	FS, A
	15M	5-14-62	27	70	218	83	FS
	6M	5-15-62	29	100	228	66	FS
	40M	5-15-62	27 $\frac{7}{8}$	94	218	66	FS
	48M	5-15-63	28 $\frac{1}{2}$	77	FS
	53M	5-15-63	28	121*	237	83	FS
	9N	5-16-64	71*	FS
	11M	5-16-62	67	FS
	14M	5-16-62	29 $\frac{1}{4}$	56	228	66	FS
	3093	5-16-64	52*	FS
Alaska Pen.	54M	5-16-63	27	65*	FS
Alaska Pen.	3094	5-16-64	45*	FS
Kodiak Is.	24M	5-17-62	22 $\frac{1}{2}$	73	200	47	FS
	34M	5-17-62	28 $\frac{3}{4}$	91	180	59	FS
	3N	5-18-64	28 $\frac{1}{8}$	111	FS
	55M	5-18-63	26 $\frac{1}{2}$	48*	FS
Alaska Pen.	3099	5-18-64	70*	FS

AND VASA DEFERENTIA OF SEXUALLY MATURE BROWN BEARS^a

General ⁵ Character	Intertubular Area		Diam. (μ)	Height of Epithel (μ)	Epididymis			Vas Deferens		
	Abundance ⁶	Cytoplasmic Vacuolation ⁷			Lumen ⁸ Contents	Coagulum ⁹ Prevalence	Cytoplasmic ¹⁰ Droplets	Lumen ⁸ Contents	Coagulum ⁹	Cytoplasmic ¹⁰ Droplets
I	+++	L	268	64	S	N	+	S, A	N	+
I	+++	L	262	67	S, E	+	+	S	+	+
IF	+	N	253	62	S, A, E	+	++	A, S	+	N
I	++	L	S, A	+++	+
I	+++	L	S	S
I	++	A	S	S
I	+++	L	279	70	S	N	+	S	N	+
IF	+	A	S	S	+	++
I	++	A	271	66	S, A, E	N	+++	S, A	N	+
I	++	A	S	N	+	S	N	N
I	+++	A	S	N	+
IF	+	A	S	S
I	+++	L, H	275	63	S	N	+	S	N	N
I	++	L	307	59	S, A	N	+++	S	N	+
I	+++	L	S	N	++	S	+	++
I	+++	L, H	S	N	++	S	N	+
I	+++	L, H	319	47	S, E	N	++	S	N	+
I	++	L, H	S	+	++
I	+++	L, H	S	+	++	S	N	+
I	+++	L, H	317	64	S, A	++	+++	S, A	N	+
I	+++	L, H	326	66	S, A	N	+	S, D	N	++
I	+++	L, H	323	80	S, A	N	+++	S, A	N	+++
I	+++	L, H	262	49	S, A	N	++	S, A	N	++
I	+++	A, H	279	59	S, A	+	+++	S, A	+	N
I	++	L, H	360	64	S	+	++	S, D, A	N	N
I	+++	L	S	N	N	S	+	N
I	++	A, H	342	71	S, A	+	+++	S, A	+	++
I	+++	L	S	N	+	S	+	+
I	++	A, H	234	59	S	+	++	S	N	+
IF	+	A, H	224	53	S, A, E	+	+	S, A	N	+
I	++	L, H	S	++	+	S
I	+++	L	S	N	N	S	N	+
I	++	A, H	243	59	S	+	+
I	+	A, H	234	63	E, S	++	++	E, S	N	++
I	+++	L	317	51	S, E	+++	N	S	N	N
I	+++	L, H	S	+	N	S	N	N
I	+++	A, H	S	+	+	S	N	N
I	+++	A, H	S	N	N	S	N	N

Table III continued on next page.

TABLE III (continued)

RESULTS OF EXAMINATIONS OF TESTES, EPIDIDYMIDES,

Location	Specimen Number	Date	Skull ¹ Meas.	Testis ³ Wt. (Gms.)	Testis Tubules		Activity ⁴ State
					Diam. (μ)	Height of Epithel (μ)	
Kodiak Is.	4N	5-19-64	48*	FS
	15N	5-19-64	59*	FS
	30M	5-19-62	25½	78	265	76	FS
	41N	5-19-64	73	FS
	51M	5-19-63	26¼	92*	247	66	FS
	64M	5-19-63	27¾	FS
	27M	5-20-62	24⅞	64	216	59	FS
	23M	5-22-62	27⅞	97	218	58	FS
	50M	5-22-63	27½	80*	266	82	FS
	52M	5-22-63	29¼	113*	264	83	FS
	17M	5-23-62	26¼	70	230	66	FS
	35M	5-23-62	28⅞	89	269	67	FS
	58M	5-23-63	69*	253	65	FS
	32M	5-24-62	28½	78	246	76	FS
	37M	5-24-62	28½	87	263	75	FS
	38M	5-24-62	28⅞	86	243	FS
	19M	5-25-62	27¾	83	294	77	FS, A
	39K	5-25-63	87*	FS
	63M	5-25-63	27¾	52*	FS
	39M	5-28-62	28	85	FS
	29M	5-29-62	27	96	285	83	FS
	68M	5-30-63	26½	FS
	62M	5-31-63	27½	FS
Alaska Pen.	E252	5-2-63	FS
Kodiak Is.	60M	6-1-63	52*	FS
	66M	6-12-63	84*	FS
Alaska Pen.	1812	7-14-63	52*	253	77	FS
	1820	7-17-63	84*	276	76	FS
	1825	7-18-63	68*	247	76	FS
	1827	7-19-63	78*	237	59	FS, A
	1831	7-21-63	52*	209	60	FS, A
	78M	8-3-63	53*	206	66	A, FS
Kodiak Is.	69M	10-1-63	25¼	FS, A
	70M	10-2-63	26⅞	FS
	42A	10-17-62	22 ¹⁵ / ₁₆	54*	184	44	FS, A
	48N	11-4-64	22¼	55*	FS, A
	55N	11-10-64	28¼	81*	199	47	SN, A
	54N	11-10-64	28⅞	56*	169	53	SN, A

^a For explanation of number designations see Table II.

AND VASA DEFERENTIA OF SEXUALLY MATURE BROWN BEARS^a

General ³ Character	Intertubular Area		Epididymis				Vas Deferens			
	Cytoplasmic Abundance ⁶	Vacuolation ⁷	Diam. (μ)	Height of Epithel (μ)	Lumen ⁸ Contents	Coagulum ⁹ Prevalence	Cytoplasmic ¹⁰ Droplets	Lumen ⁸ Contents	Coagulum ⁹	Cytoplasmic ¹⁰ Droplets
IF	++	A, H	S	N	N	S	N	N
I	+++	L, H	S	N	N	S	N	N
I	+++	A, H	267	52	S, A	N	+	S	N	+
IF	++	A, H	S	N	+	S	N	N
I	+++	L, H	293	63	S, E	N	+	S	N	+
I	++	A, H	S	N	N	S	N	N
I	++	A, H	253	59	S	+	++	S	+	+
I	+++	L, H	275	68	S	+++	+
I	+	A, H	360	71	S	+	+	S	N	+
I	+++	L	333	56	S	++	N	S	N	N
I	+++	L	325	67	S	N	+	S	N	N
I	+++	A, H	317	63	S	+	+	S	N	+
I	++	A, H	298	64	S	N	+
I	+++	A, H	309	71	S	N	+	S	N	N
I	++	A, H	326	71	S, E	+	+	S	N	+
I	+++	L, H	288	64	S, A	++	+	S, A	N	+
I	+++	L, H	355	74	S, A	N	N	S	N	N
I	++	A, H	S	+	+	S	N	+
I	+++	A, H	S	N	+	S	N	N
I	++	A, H	S, A	N	C	S	N	N
I	+++	L, H	271	62	S	N	+	S	N	+
I	++	A, H	S, E
I	+++	L, H	S	N	N	S	N	N
I	++	A, H	S	N	N
I	+	A, H	S	N	N	S, D	N	N
I	+++	L	262	62	S	N	N	S	N	N
I	++	A, H	271	63	S	N	+	S	N	N
I	+++	A, H	261	66	S	N	+
I	++	A, H	S	N	+	E, S	N	+
I	++	A, H	S, E	N	N	E, S	N	N
I	++	A, H	253	66	S, A	+	+	S, A	N	N
IF	+	A, H	224	64	S, A, D	+	+
....	S, A
....	S	S
I	++	A, H	234	59	S, D, A	N	+
IF	++	A, H	A, S	+	+	A, D, S	N	N
I	++	L	215	59	A, D, S	++	N	A, D, S	N	N
IF	++	A, H	262	39	A, S, D	++	+	E, A, D, S	N	N

The reproductive tracts of six bears were of known approximate age as established on the basis of returns from animals live-trapped and marked as cubs or yearlings (Troyer, *et al.*, '62). The remaining specimens were estimated as to sexual status on the basis of skull sizes, and testicular weight and histological comparisons with the known-age animals.

Male reproductive tracts were removed, the testes dissected free from the tunica vaginalis, and the epididymides and proximal segments of the vasa deferentia left in contact with the testes (Pl. I, figs 1-3). When possible the testes were weighed fresh; otherwise, the fixed weight was determined and adjusted to the fresh weight (Table II). The specimens were fixed in 10 percent formalin and stored in 70 percent ethyl alcohol. Histologic sections of all specimens were prepared from the body of the epididymis together with the underlying portion of the testis and the adjacent portion of the vas deferens, where available, and from other areas of the reproductive tract for representative specimens.

Sperm morphology and maturation were determined by examining sperm taken from various areas of preserved epididymides and vasa deferentia. The sperm were stained in a 1 percent solution of osmium tetroxide and the anatomical features of whole preserved sperm were then studied and measured with the light and electron microscope.

The data available for the specimens studied are listed in Tables I to III. The specimens were classed as being infantile, prepuberal, or sexually mature as determined from histological findings. Infantile specimens exhibited little or no spermatogenic activity. Prepuberal specimens showed some spermatogenesis but not to a sexually functional state. Sexually mature bears represented one of three reproductive states: (1) preseasonal—namely animals recovering from a nonbreeding period; (2) sexually active—bears in or near full breeding condition; or (3) post-seasonal—animals showing spermatogenic decline following the breeding season.

Included for each specimen, if available, are the collection date, an age classification, body weight, testicular weight, the combined length plus zygomatic width of the skull, and the histologic classification of the testis, epididymis, and vas deferens (Tables I to III).

OBSERVATIONS

Estimates of Age and Reproductive State

Reliable procedures for estimating the ages of bears are not available. Nonetheless the specimens included in this study were readily identified as infantile, prepuberal, or adult on the

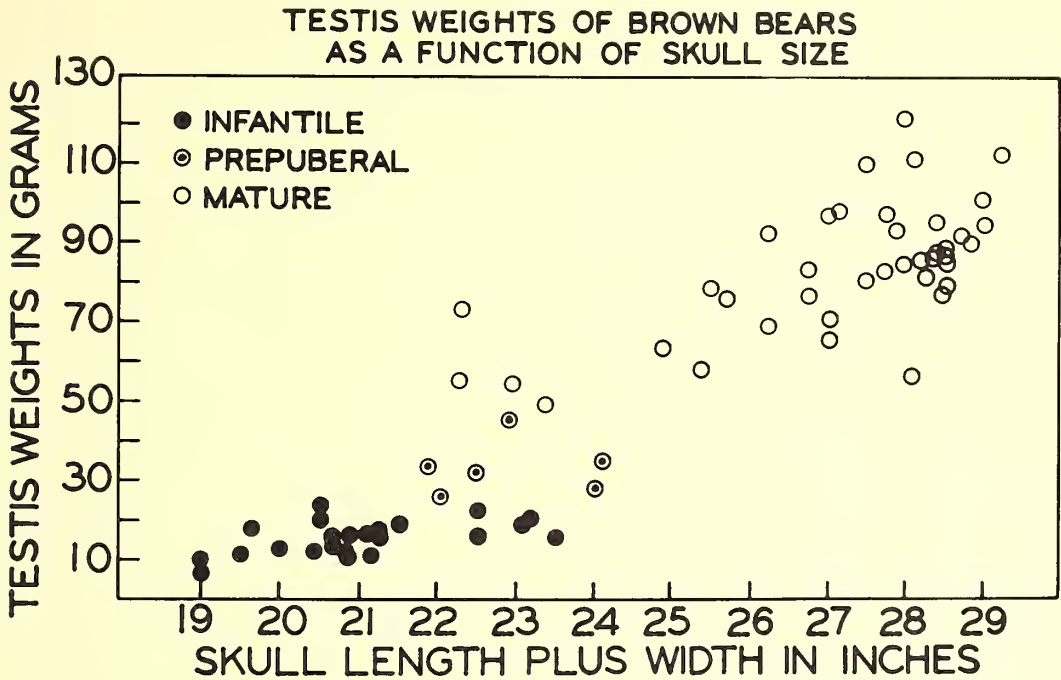
basis of testicular histology. It early became apparent, too, that skull sizes and testicular weights might also provide useful criteria for determining the reproductive maturity of bears and for estimating their approximate ages, at least in younger animals.

As seen in Text-figure 1 and Tables I to III, the size of the brown bear's testis appears to be directly correlated with the size of the skull and thus, presumably, with age. Although there are individual and seasonal variations, it will be noted that single testes of mature specimens range upward in weight from approximately 50 gms; those of infantile bears weigh approximately 25 gms or less. The limited known-age specimens available (Table I) suggested that the infantile group included bears to three years and occasionally older. The sexually mature specimens were presumably four or more years of age. The testis weights of presumed prepuberal bears based on histological examination were found to fall roughly between those of the infantile and sexually mature animals but overlapped each group slightly (Text-fig. 2 and Tables I to III). The overlap is attributed to the different ages at which individual male bears attain sexual maturity. Dittrich and Kronberger ('63) have reported similar variations in the time of sexual maturity in the female brown bear.

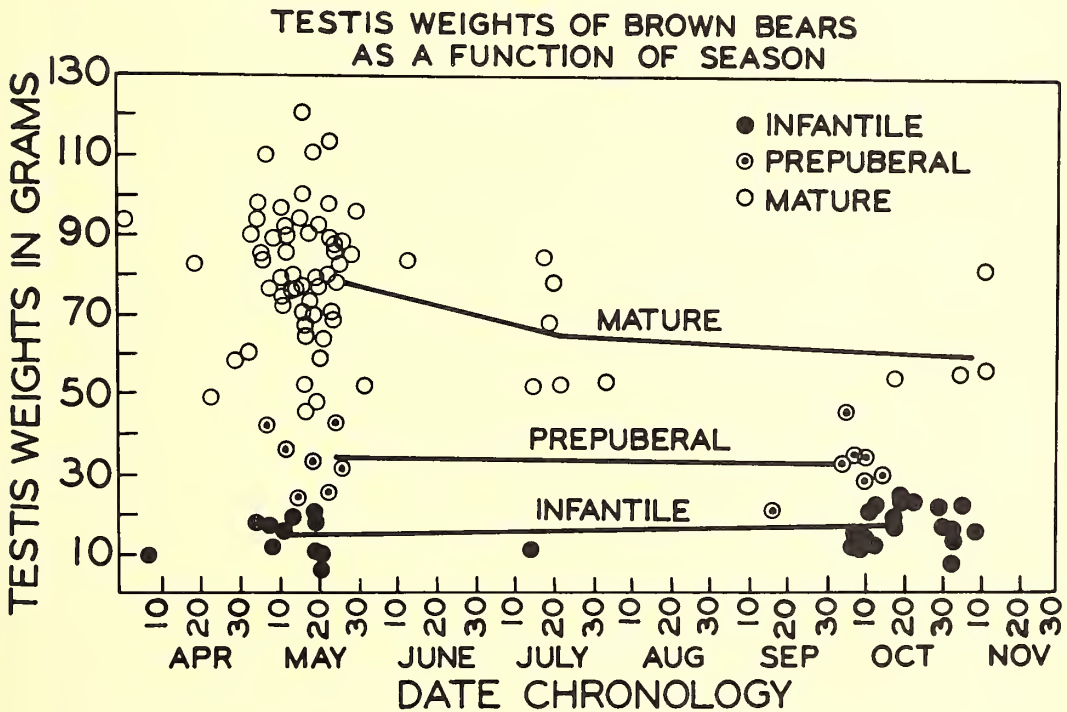
Most male bears apparently attain prepuberty in their fourth year and became sexually mature at approximately four and one half years of age. Presumably, as judged by the widely divergent skull sizes of prepubal bears a few attain this state in their third year and others not until their fifth year (Tables I to III and Text-fig. 1). The four sexually mature specimens with skulls measuring only 22 and 23 inches in length plus width and separate from the remaining mature animals, and the five infantile bears with skulls in the same size range and separate from the remaining infantile specimens, provide further evidence that the age of puberty is quite variable among male bears (Text-fig. 1).

The relative age and sexual status of bears may also be judged with fair accuracy from the skull (Tables I to III and Text-fig. 1). Animals with combined skull length and width measurements exceeding 24½ inches are quite assuredly sexually mature specimens exceeding four years of age. Conversely, specimens with skulls measuring less than 22 inches are, generally, immature. Between these limits is a group of bears of mixed sexual status, the majority presumably being prepuberal animals in their fourth year of life (Tables I to III and Text-fig. 1).

While paired testes were obtained from only a few bears, there was no indication that signi-



TEXT-FIG. 1. Testis weights of brown bears as a function of skull size.



TEXT-FIG. 2. Testis weights of brown bears as a function of season.

ficant differences existed between left and right testicular weights in the brown bear (Table III). The heaviest testis weighed 121 gms. The mean testis weight was 80 gms for the sexually mature bears, 31 gms for the prepuberal bears, and 12 gms for the infantile bears. There were, however, seasonal variations in the testicular weights of bears. Among sexually mature specimens heaviest testes occurred during the breeding season in May and June (Table III and Text-fig. 2). Testicular weights were then approximately one-third greater than during the fall postbreeding season, and conceivably at least twice as heavy as at the time of maximum testicular regression in mid-winter. The decline in weight is in large measure attributable to shrinkage of the seminiferous tubules during the nonbreeding season (Table IV). A similar condition has been reported in the black bear (Erickson and Nellor, '64). In contrast to the spring to fall testicular weight decline in the adult bear, an opposite condition occurs in the infantile bear. Here, fall testicular weights exceed spring weights presumably because the infantile bear realizes substantial body growth during the spring to fall period. It follows, therefore, that the fall testes of this sexual class would weigh more since, as was shown in Text-figure 1, a positive correlation exists between the body size and the testicular weight of bears. There is a suggestion, nonetheless, that the seminiferous tubules of the infantile bear undergo slight shrinkage during the postbreeding season as in the mature animal (Table IV).

In contrast to both the infantile and adult bear, the testes of prepuberal bears remain es-

entially constant in weight from spring to fall (Text-fig. 2). This is presumably due to slight shrinkage of the seminiferous tubules following the breeding season in the spring, but this is accompanied by some compensatory growth of the body as a whole (Table III and compare Pl. III, fig. 12 and Pl. IV, fig. 19).

Gross Features of the Male Reproductive Tract

Grossly the reproductive tract of the male brown bear differs only in relative size from that described for the black bear (Erickson and Nellor, '64). The species has a well-developed os penis which measures up to eight and one-half inches in length in older bears and, as in the black bear, the penis is capable of extrusion from its sheath only with the attainment of sexual maturity. The testes are scrotal from infancy and are held closely to the body except in the adult animal during the breeding season. They are then further removed from the body due apparently to relaxation of the scrotum and their enlargement through vascular engorgement and tubule hypertrophy (Table IV, and Pl. I, figs. 1 and 2). Concomitant with the attainment of sexual maturity the tip of the scrotum becomes bare and very darkly pigmented. The hair-free patch is reduced in size and less obvious in late fall animals due principally to scrotal shrinkage. However, once sexual maturity is attained complete refurring of the patch apparently does not occur since it was observed in bears killed from April through November. This character is thus a useful one for identifying sexually mature bears.

TABLE IV
TESTIS TUBULE AND EPIDIDYMAL DUCT MEASUREMENTS OF
BROWN BEARS AS RELATED TO AGE AND SEASON ^(a)

Season	Reproductive Status					
	Infantile		Prepuberal		Mature	
	No. Spec.	Ave. Diam. (u)	No. Spec.	Ave. Diam. (u)	No. Spec.	Ave. Diam. (u)
Spring (Apr. 2-May 29)						
Tubule Diam.	4	97	5	159	31	245
Epididymal Duct Diam.	5	163	4	218	34	293
Summer (June 12-Aug. 3)						
Tubule Diam.	1	83	—	—	6	238
Epididymal Duct Diam.	—	—	—	—	5	254
Fall (Sept. 1-Nov. 11)						
Tubule Diam.	11	94	4	145	3	184
Epididymal Duct Diam.	11	180	4	199	3	237

^(a) Includes only specimens whose tissue condition warranted measurements; average of five epididymal and 10 tubule measurements.

The testis of the brown bear is roughly ovoid in shape and is slightly compressed laterally (Pl. I, figs. 1 and 2). The organ is not particularly large for the animal's size. In the adult bear at the height of the breeding season it measures approximately 9 x 6 x 5 cm and weighs slightly over 80 gms. Three bears, 1821, 1827, and 1831 had body weights of 705, 630, and 560 pounds and testis weights, respectively, of 84, 78, and 52 gms. The epididymis of the bear is large and tightly attached to the dorso-lateral surface of the testis, as is the vas deferens which courses back along the epididymis (Pl. I, figs. 1 and 2).

The gross internal architecture of the testis is shown in Plate I, figure 3. The fibrous tunica albuginea is very heavy. The blood vessels of the tunica vascularis hypertrophy markedly during the breeding season and supply the major blood needs of the testis. The vascularis layer is most pronounced at the cephalic end of the gland, becoming diminished caudally as vascular elements are passed into the testis (Pl. I, fig. 3).

At the cephalic end of the testis portions of the tunica albuginea pass into the gland as the mediastinum testis, which consists of a core of fibrous connective tissue, minor blood vessels, and the rete testis. The mediastinum testis is central in position and extends approximately three-fourths of the length of the testis (Pl. I, fig. 3). This is continuous with finer laminae of connective tissue, the septulae testis which extend radially into the testis encompassing the individual lobuli testis, the germinative, and endocrine portions of the gland. The coiled seminiferous tubules connect with short, straight tubuli recti which convey the sperm from the apex of the lobules to a series of irregular spaces lined with low cuboidal epithelium, the rete testis, which extends throughout the mediastinum (Pl. IX, fig. 51).

The Histology of the Male Reproductive Tract

Infantile bear.—The seminiferous tubules of the infantile bear are simple, undifferentiated cords widely dispersed in a cellular connective tissue. There is little apparent change in their appearance in most bears until the animals reach two years of age (Pl. II, figs. 4 and 5). The seminiferous tubules then show marked enlargement and come to occupy a major portion of the testis mass (Pl. II, fig. 6). The tubules of the two-year-old bear at the time of the breeding season in May measure slightly less than 100 μ in diameter, are lumenless and filled with an amorphous material of uncertain origin—possibly Sertoli cell cytoplasm. The epithelial membrane of the tubules is two to four cells thick and for the most part the cells resemble Sertoli cells with promi-

nent nucleoli (Pl. II, fig. 6). However, certain cells are hypertrophic and show mitosis indicating that some among them are germ cells. These do not develop beyond spermatocyte stages, however, and they either degenerate in situ or are passed to the tubule center, become pyknotic, and disintegrate. Relatively few of these immature cell forms are passed to the epididymis and the vas deferens (Pl. II, figs. 7 to 9).

The interstitial cells of the two-year-old bear are abundant but the tissue occupies a minor portion of the testis. The cells contain relatively little cytoplasm, are crowded closely together, and the nuclei stain darkly (Pl. II, fig. 6). It is noteworthy, nonetheless, that bears of this age class apparently produce abundant androgen as indicated by the well-developed epididymis and vas deferens (Pl. II, figs. 7 to 9). These organs appear fully functional, the epithelium being pseudostratified columnar with stereo-cilia as in the typical sexually mature mammal. With rare exceptions, however, the epididymal ducts and the vasa deferentia are empty of spermatogenic elements during the spring breeding season (Pl. II, fig. 7). On the other hand, abundant secretion products and an amorphous coagulum are constant in these organs at all seasons (Pl. II, figs. 8 and 9).

Following the breeding season in spring, the reproductive tract of the two-year-old infantile bear shows slight retrogressive changes. By October the seminiferous tubules undergo some shrinkage. This is indicated by thickening and wrinkling of the basement membranes, and an increased density of the central cytoplasmic complex (Pl. III, fig. 10). There is also a decline in the cell population of the seminiferous tubules and an accompanying increase in pyknotic shed elements, although this was highly variable between bears. As in the spring infantile bear, most of the cells lining the basement membrane are Sertoli-like (Pl. III, fig. 10).

The intertubular tissue in the two-year-old fall infantile bear was more apparent than during the spring, was frequently arranged in strands, and the cytoplasmic-nuclear ratio of the Leydig cells was slightly greater (compare Pl. II, fig. 6 and Pl. III, fig. 10). In general, however, the histology of the testis of the two-year-old bear does not differ appreciably from spring to fall.

The same statement cannot be made for the epididymis and the vas deferens. By November these organs undergo marked retrogression from their highly active state during the spring (compare Pl. II, fig. 7 and Pl. III, fig. 11). By late fall the ducts become reduced in size, lose their cilia, and develop a thick, dense, connective tis-

sue coat. While most of the ducts are empty, a few contain abnormal and immature sperm cell elements, and a heavy coagulum is a common feature (Pl. III, fig. 11).

Prepuberal bear.—Unfortunately no prepuberal bears were obtained prior to the breeding season in May. However from this time on there was a marked increase in the size of the seminiferous tubules to approximately 160μ (Table IV) and the development of large, distinct tubule lumina (Pl. III, fig. 12). The interstitial tissue at this time appeared sparse and compressed between the swollen tubules. The Leydig cells seemed to have a slightly greater cytoplasmic-nuclear ratio than in the infantile spring bear (compare Pl. II, fig. 6 and Pl. III, fig. 14).

While the germinal epithelium of the spring prepuberal bear was only four or five cells thick, there was a considerable amount of spermatogenic activity and spermatogenic stages were quite readily differentiated from Sertoli cells (Table I, Pl. III, fig. 13 and Pl. V, fig. 24). Interestingly, however, spermatogenesis became arrested in the secondary spermatocyte and spermatid stages and, as in the infantile bear, the majority of these cells appeared to disintegrate in situ. A fair proportion were shed to the tubule lumina, however, and passed to the epididymis and vas deferens (Pl. III, fig. 15 to Pl. IV, fig. 17). In this process multinucleate giant cells were often formed (Pl. III, figs. 13 and 15), apparently by a coalescence of developing germ cells in situ or a failure of the cell clones to separate (Fawcett, 1961). These are thought to indicate an animal in less than full reproductive vigor (Parks, '60).

As with the two-and-one-half-year infantile bear, the epididymis and vas deferens of the spring prepuberal bear is well developed with abundant secretory products (Pl. IV, figs. 16 and 17). The diameters of the ducts are increased, however, over those of the infantile animal (Table IV). A notable difference from the infantile bear is the regular occurrence of immature and abnormal cell forms within the ducts (Pl. III, fig. 15). Relatively few of these reach the vas deferens which suggests that their degradation is continuous as they proceed down the tract (Pl. IV, figs. 16 and 17).

Following the breeding season the seminiferous tubules of the prepuberal bear show a loss of turgor and activity (Pl. IV, fig. 18). The tubules become reduced in diameter (Table IV), the basement membranes thicken and wrinkle, and the tubule lumina are markedly reduced (Pl. IV, figs. 19 and 20). This is accompanied by a reduction in the germinal epithelium to the point that Sertoli cells predominate over germ cells. Nevertheless spermatogenesis continues at

a diminished rate, the formed elements continuing to degenerate either in situ or in passage to the tubule lumina and epididymal ducts.

Ultimately, during late fall, defoliation of the spermatogenic epithelium becomes so pronounced that the only cells remaining within the tubules appear to be Sertoli cells (Pl. IV, figs. 19 and 20). During spermatogenic decline, as during other stages of the cycle, not all bears or even all tubules of a given bear were in the same reproductive state (Pl. IV, figs. 18 and 20). These differences were not attributable to the "spermatogenic wave" phenomena.

During the declining phase of spermatogenesis in the prepuberal bear the interstitial tissue is strandlike, shows an apparent increase in cytoplasmic amount, and the Leydig cell nuclei are smaller and darker stained (compare Pl. III, fig. 14 with Pl. IV, figs. 19 and 20). This is accompanied by atrophy of the vas deferens and of the epididymis (Pl. IV, fig. 21 to Pl. V, fig. 24). The vas deferens is the first of these organs to undergo degenerative changes (Pl. V, figs. 23 and 24). Its decline precedes even that of the seminiferous tubules (compare Pl. IV, fig. 19 and Pl. V, fig. 24).

The first indication of retrogression of the vas deferens and epididymis is disorganization of the duct epithelia (Pl. V, fig. 23). This process becomes marked and is accompanied by a decrease in the size of the ducts (Table IV). By November the epithelium of the vas deferens is reduced to a layer of very low columnar cells, the primary duct contents being degradation products of the earlier pseudostratified epithelium, a few abnormal germinal elements, and coagulum (Pl. V, fig. 24). By contrast, the epididymis retains a functional appearance for at least an additional month (Pl. IV, fig. 21 and Pl. V, fig. 22) and in none of the prepuberal specimens available to us did the epididymis attain a state of involution similar to that shown by the vas deferens (Pl. V, fig. 24). Conceivably, however, such a state would have been seen if we had had specimens of this group extending beyond early November. A notable feature during the declining phase was a marked increase in the coagulum found within the ducts (Pl. IV, fig. 21 and Pl. V, fig. 22).

The Sexually Mature Bear

Redevelopment phase.—The earliest mature spring bear, 41 M, was taken April 2, 1963 (Table III). The activity state of this animal was, however, well advanced over a number of other specimens taken at later dates. Of particular interest among these was specimen 22 M taken April 22, 1962. The small size of this animal's skull, and its delayed spermatogenic

state as compared with a majority of the other mature specimens we examined, suggest that it was just attaining sexual maturity (Table III and Pl. V, figs. 25 and 26). Among the obviously sexually mature bears included in our collection, specimen 42 M taken April 18, 1963, exhibited the least advanced stage of spermatogenic development (Pl. V, fig. 27). The seminiferous tubules of this specimen appeared quite uniformly rounded and the surrounding intertubular tissue was stringy and loose. This suggests that the tubules were not as markedly swollen as later in the cycle. In general appearance the tubules were quite dense, and without a distinct lumen. They were densely packed with developing spermatocytes and spermatids (Pl. VI, fig. 28). A few tubules were, however, in a more advanced state and exhibited all stages of spermatogenesis including mature spermatozoa (Pl. VI, fig. 29).

In the redeveloping bear testis abnormal cell forms were frequently observed, particularly multinucleated giant cells (Pl. VI, fig. 30). The high frequency of abnormal and immature germinal elements seen in the epididymides and vasa deferentia of the late redeveloping bears suggests that the first germinal elements passed are largely nonviable forms (Pl. V, fig. 26, Pl. VI, figs. 29 and 33). A heavy coagulum was also regularly noted in the lumina of the redeveloping tubules (Pl. V, fig. 27, Pl. VI, figs. 28 and 30). This was probably in part Sertoli cell cytoplasm together with degradation products of abortive germinal elements phagocytosed by Sertoli cells (Vilar, '65).

The interstitial tissue of the redeveloping bear testis is abundant. The cells have a relatively large cytoplasmic-nuclear ratio and the abundance of large vacuoles in their cytoplasm is striking (Pl. VI, figs. 28 and 29).

While specimens of bear epididymides and vasa deferentia were not available from bears prior to late testicular redevelopment, the well-developed state of these organs from the earliest specimens available suggested that they became fully functional before the testes produced sufficient mature spermatozoa for fertile breeding (Pl. VI, figs. 31 and 32). And, as indicated earlier, immature and abnormal cell forms were regularly to be noted in the duct contents of the redeveloping bear epididymis and vas deferens. A further interesting character was a heavy and marked vacuolation of the epithelia of the epididymis and vas deferens. This is possibly a precursor of the abundant secretion products noted in these organs (Pl. VI, fig. 32).

Fully active animals.—As has been mentioned earlier, bears vary markedly in the time of at-

tainment of full breeding condition. Apparently, however, all mature specimens are reproductively capable in May (Table III).

At the height of breeding capability the seminiferous tubules are much swollen and compressed together and thus appear flattened or polygonal in cross section (Pl. VII, fig. 34). The tubules have distinct lumina and all stages of spermatogenesis are to be seen in the germinal epithelium. Abnormal sperm are rarely noticed. While tufts of maturing spermatozoa are abundantly embedded in the cytoplasm of Sertoli cells, free sperm are seldom noticed in the tubule lumina which suggests their rapid transport to the epididymis (Pl. VII, fig. 34). The tubule lumina are also free of the amorphous coagulum which was commonly noted in the redeveloping bear.

At the height of the breeding season the intertubular interstitial tissue of the mature bear appears sparse and dense (Pl. VII, fig. 34). The large, abundant cytoplasmic vacuoles noted in the interstitial tissue of the redeveloping bear are generally not noticed at this time except in the abundant interstitial tissue which invades the tunica albuginea and septulae testis (Pl. VII, figs. 38 and 39).

The epididymis and vas deferens of the brown bear at the height of the breeding season are greatly distended with sperm (Pl. VII, figs. 35 and 36). That the vas deferens, as well as the epididymis, is an important organ for sperm storage in this species is indicated by the fact that it becomes so distended with spermatozoa that the usual pseudostratified columnar epithelium becomes low columnar (Pl. VII, fig. 36). At the height of the breeding season abnormal or immature cell forms occur only rarely in the ducts, and the epithelium of the epididymis and vas deferens are largely devoid of the heavy vacuulations noted in the prepuberal and in the preseasonal mature bear (Pl. VII, figs. 35 and 36). Bleb-like secretions are frequently to be seen however at the tips of the stereocilia (Pl. IV, fig. 6). The source of these is presumed to be the abundant vacuoles noted in the epithelia of the vasa deferentia and epididymides of the seasonal adult and prepuberal bear, and they are further the apparent source of the abundant secretions noted among the stereocilia in these animals (Pl. IV, fig. 17 and Pl. VI, fig. 32). It would appear, therefore, that there is a build-up of secretion products during the nonbreeding period and that the release of these products exceeds their build-up during the breeding season.

Postseasonal animal.—Following the limited breeding season in the spring, the male brown

bear shows spermatogenic decline. The time of the decline varies widely between bears (Pl. VII, figs. 37 and 39). The first sign of seminiferous tubule atrophy is the appearance of considerable numbers of abnormal and immature cell forms (Pl. VII, figs. 37 and 38). Spermatogenesis continues but is arrested in the secondary spermatocyte and spermatid stages. This condition closely parallels spermatogenesis as it occurs in the prepuberal and the preseasonal mature bear, particularly as regards the formation of multinucleated giant cells (Pl. III, fig. 13; Pl. IV, fig. 18 and Pl. VI, fig. 30). During the early phases of decline the germinal epithelium becomes reduced to four or five cells in thickness and tubule lumina become more distinct (Pl. VII, fig. 39 and Pl. VIII, fig. 40). This is followed by tubule shrinkage as manifested by a reduction of the luminal and a thickening and folding of the basement membranes (Pl. VII, fig. 38 and Pl. VIII, fig. 42). Defoliation of the spermatogenic epithelium continues until ultimately many, if not most, of the tubules are reduced to simple cords, the sole cell population of which consists of a single layer of cells lining the basement membrane as in senile testes (Pl. VIII, figs. 41 to 43). As in the prepuberal bear during the postbreeding season, these cells appear to be Sertoli cells.

Since we had no specimens extending beyond November, it was not possible to determine how complete seminiferous tubule decline becomes. The indications are, however, that the condition becomes quite general at the height of decline, presumably in midwinter when the animals are in their winter dens.

The interstitial tissue of the mature bear testis during the late postbreeding period appears slightly more abundant than during the breeding season. There is an apparent increase in the amount of cytoplasm within the cells but the vacuoles do not appear to attain the size of those seen during the prebreeding season (compare Pl. VI, figs. 28 and 29 and Pl. VIII, figs. 40 to 42). The interstitial tissue at this time is strand-like, the nuclei being dense and dark staining, and intercellular spaces are common. While these spaces were perhaps in part artifacts, we believe they represent decreases in cell size possibly coupled with edema. Concomitant with seminiferous tubule atrophy during the postbreeding season in the adult bear there is an accompanying but slightly later decline of the vas deferens and the epididymis (Pl. VIII, fig. 44 to Pl. IX, fig. 49). This is suggested by the appearance of immature and abnormal cell forms in the ducts before any discernible change in the histology of these organs. The passage of aberrant forms continues and ultimately they

predominate over normal forms in the duct contents (Pl. VIII, fig. 45). This is accompanied also by a marked reduction in the sperm load. In some instances the epididymal ducts are largely empty of germinal elements before there is any recognizable gross change in the epididymis itself (Pl. IX, fig. 46). In other cases some disorganization of the epithelium lining the epididymal ducts becomes obvious while germinal elements are still evident. Surprisingly, however, the vas deferens declines well in advance of the epididymis (compare Pl. VIII, fig. 45 and Pl. IX, fig. 48), the epithelium becoming low cuboidal and the duct contents consisting solely of degradation products and degenerate sperm (Pl. IX, fig. 48). In certain specimens such a condition occurred as early as September while in others a fairly healthy condition existed as late as November (Table III).

The limited number of fall specimens available to us did not afford a complete picture of epididymal decline in the adult bear. It appears likely that at the height of decline the epithelium of the epididymis roughly resembles that attained by the vas deferens. It is certain that during this time there is a marked reduction in the diameter of the epididymal ducts together with a relative increase in the connective tissue surrounding them (Table IV and Pl. IX, fig. 49).

Sperm morphology.—Mature brown bear spermatozoa appear typically mammalian in form with an overall length of 78.2μ . The head of the sperm is round to oblong in greatest length-width aspect, and flattened with a slight inflection of the head tip. The length and width of the head are 7.4 and 4μ respectively. The cylindrical midpiece measures 11.5μ and in sperm taken from the epididymis it typically retains a midpiece cytoplasmic droplet (Pl. IX, fig. 50). The attachment of the midpiece to the head is slightly abaxial. The length of the tail is 57.0μ and the length of the terminal fibrilis 2.3μ . These measurements fall within the range of values reported for other mammalian species (Parkes, '60).

DISCUSSION

Although criteria for estimating the ages of brown bears have not been developed, several characters discussed in this study appear to have merit as indices for estimating the reproductive status and age of the male bear. The histology of the testis, regardless of the season, appears definitive for establishing the sexual status of bears as being infantile, prepuberal, or sexually mature. While a more extensive collection of known-age specimens is necessary to determine more closely the ages represented by each sexual group, these preliminary data suggest that the infantile class is represented by bears less than

three years of age and the sexually mature class by bears four years and older. The prepuberal class is mostly bears in their third year of life, although a few two-year and four-year animals are believed to be included also.

The weight of the testis and the size of the skull appear equally useful as indices of the age and sexual status of male bears. As judged from the histology of the testis, infantile bears generally have single testis weights of less than 25 gms and skulls measuring less than 22 inches in length plus width. Conversely, the single testis weights of sexually mature bears ranged upward from approximately 50 gms and the skulls seldom measured less than 24½ inches in length plus width. The testes and skulls of prepuberal animals lie roughly between those of the infantile and sexually mature groups with some slight overlap with both as was also true for the histological classifications. Nonetheless, skull sizes and testicular weights, particularly if taken together, appear to be fairly reliable criteria for classifying bears as to sexual status and relative age (Text-fig. 1). Other criteria described as useful for identifying the sexually mature bear were: capacity of the penis to be manually extruded from its sheath, and the presence of a darkly pigmented hairless patch at the tip of the scrotum.

These studies show that the male brown bear is a seasonal breeder, the reproductive period beginning before and extending beyond the breeding season of the female. As contrasted with the more limited and consistent reproductive period of the female, that of the male appears to last four or five months and varies markedly between individual bears. Certain specimens are in full reproductive vigor well in advance of the time of peak breeding while others appear reproductively capable until near the time of denning in November.

It seems, therefore, that the male brown bear has a potential breeding season slightly exceeding half of the year and encompassing the greater portion of the den-free period. The differing testicular histology throughout this period suggests, however, that individual bears are sexually capable for perhaps only about half of the potential breeding period (Table I). It is significant that during the period of normal female reproductive activity from late May to early July (Dittrich and Kronberger, '63) practically all sexually mature bears are producing abundant spermatozoa (Table III).

From a comparative point of view, certain aspects of the morphology and histology of the brown bear reproductive tract are extremely interesting. The high development of the epididymis and the vas deferens of the immature

one-and-two-year old bear well in advance of any spermatogenic activity was remarkable and was seemingly typical of the state attained by the sexually mature animal. To our knowledge such an advanced state of development at least two years in advance of the attainment of sexual maturity is unique among mammals studied to date with the exception of the closely related black bear (Erickson and Nellor, '64). The high degree of spermatogenic activity attained by the prepuberal bear a full year in advance of sexual maturity was similarly striking.

Perhaps the most interesting feature of the histology of the male bear's reproductive tract is the marked atrophic state exhibited by the testis in the nonbreeding season. While the specimens available to us did not permit a determination as to how general the atrophic state becomes, the indications were that the senile appearance of the seminiferous tubules becomes quite general at the height of decline, presumably in midwinter when the animals are in winter dens. This was suggested both by the almost complete atrophy of the tubules during the nonbreeding season in the seasonally quite active prepuberal bear (Pl. IV, figs. 18 and 19), and by the large proportion of senile tubules in the late declining adult bear (Pl. VIII, figs. 42-44).

In light of this it appears warranted to speculate as to the manner in which the germinal epithelium becomes repopulated; whether it be from a far advanced or more limited state of atrophy. Three explanations may be advanced. First it may be that the Sertoli-like cells remaining in the tubules are really a mixture of spermatogenic and Sertoli cells but are not recognizably different. A second postulate is that the cells are truly a single cell type but bipotential. The third possibility is that portions of the tubules fail to undergo the marked atrophy indicated in Pl. VIII, figs. 41 to 43 and these residual centers repopulate the tubules. Of these possibilities the latter appears the most plausible for the following reasons: As indicated in Pl. VIII, figs. 41 and 43, wide variations were seen between the condition of tubules not only between bears but even within a given testis. Even in animals showing a high percentage of senile-type tubules, other tubules could be found showing active spermatogenesis. It was interesting too that seminiferous tubule decline appeared in some cases to be affecting only individual tubules (Pl. VIII, fig. 41), but in other cases whole lobuli testes (Pl. VIII, fig. 43). This is taken as evidence that atrophy begins at given points within the tubules and then spreads progressively along their length.

We believe that seminiferous epithelial repop-

ulation (postulate 1) cannot be explained as resulting from a mixture of cells in which spermatogonia and Sertoli cells are indistinguishable. The irregularly spherical shape of the nucleus and the large, dark-staining, eccentrically located nucleolus is typical of Sertoli cells. None of these nuclei showed a condition suggestive of meiosis which further reduces the possibility of their being spermatogonia, and therefore also lowers the probability that they are bipotential as suggested by postulate two.

Another interesting feature of the histology of the brown bear testis is the marked degree to which the interstitial tissue invades the tunica albuginea (Pl. VII, fig. 39). Furthermore, the Leydig cells in these areas have a relatively large cytoplasmic-nuclear ratio, in which their large vacuoles are an important factor. Then too, while the intertubular interstitial tissue of the fully active animal appears to possess a much lower cytoplasmic content than at other times in the cycle, the cells in the tunic consistently maintained their seemingly high functional state.

The secretion products of the epididymides and vasa deferentia are apparently proliferated from their highly active stereo-ciliated epithelial cells, and vary in amount between bears. In the prepuberal bear at all seasons, and in the pre-seasonal and early postseasonal sexually mature bear, the basal cells of the epithelia of these organs commonly contain large numbers of vacuoles (Pl. VI, fig. 32). A similar state is rarely seen in the fully active animal. Rather the vacuoles appear at this time to have migrated toward the apical ends of the cells and the frequently observed bleb-like formations among the stereocilia may be a product in some way related to them. This sequence suggests a build-up of these products during the nonbreeding season and a depletion (over build-up) during the active reproductive period.

The abundant coagulum throughout the tract is apparently of varied origin and again appears to be related to the reproductive state of the animal. It seems to be absent in the fully active adult, present in low amounts in the prepuberal animal, and quite abundant in the seasonal adult, particularly during the preseasonal period (Pl. IX, fig. 46.) While some of this material may conceivably be of Sertoli cell origin, the larger amount appears to be degradation products of degenerate sperm cells phagocytized by Sertoli cells (Vilar, '65) and possibly by lymphocytes. Further degradation of degenerate sperm appears to occur in the epididymis and vas deferens and adds to the coagulum load in these organs. Additional coagulum is believed to be added to the ducts of the epididymis and the vas deferens by liquifaction of the secretions of these organs

and by the addition of cytoplasmic material from maturing sperm.

An additional interesting observation in the declining bear is the frequent invasion of lymphocytes into and surrounding the seminiferous tubules, the epididymides, and deferent ducts. A similar condition frequently occurs in the prepuberal and preseasonal adult bear (Pl. IV, fig. 19 and Pl. VIII, fig. 45). While this condition would normally suggest a pathologic state, it is too general throughout our specimens to be attributed to this. A possible explanation is that the lymphocytes are involved in the breakdown of both the epithelial debris from the ducts and of the great numbers of degenerate germinal cells.

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EXPLANATION OF THE PLATES

PLATE I

- FIGS. 1 & 2. Whole testis of a fully active bear showing well-developed epididymis and vas deferens. E-305, 5/11, X2/5.
- FIG. 3. Internal architecture of the active testis. E-305, 5/11, X9/16.

PLATE II

- FIG. 4. Testis of a one and one-half-year infantile bear during the breeding season. Seminiferous tubules are undifferentiated cords widely dispersed in loose cellular connective tissue. 65M, 5/21, X27.
- FIG. 5. Testis of a one and one-half-year infantile bear during the postbreeding season. Seminiferous tubules occupy a greater portion of the mass of the testis than in Plate II, figure 4, and the intertubular tissue shows slightly greater interstitial cell abundance. 46N, 1-1/2, X34.
- FIG. 6. Testis of a two and one-half-year infantile bear during the breeding season. Seminiferous tubules are enlarged, lumenless, and occupy a major portion of the testis. Epithelial lining is two to four cells thick. The nuclei of most of these cells resemble Sertoli cell nuclei; however, a few cells hypertrophy and undergo cell division but degenerate. Interstitial cells are relatively abundant but contain little cytoplasm and, consequently, occupy a minor portion of the testis. 12M, 5/7, X67.
- FIG. 7. Well-developed epididymis of the two and one-half-year bear during the breeding season. The ducts are characteristically free of germinal elements. 12M, 5/7, X67.
- FIG. 8. Abundant secretion products are common in the nondegenerate epididymis of the two-year infantile and prepuberal bear, and in the preseasonal and early postseasonal adult bear. 18M, 10/31, X107.
- FIG. 9. Amorphous coagulum is common in the nondegenerate vas deferens of the two-year infantile and prepuberal bear, and in the preseasonal and early postseasonal mature bear. The presumed origin of the material is liquefaction of secretion products and the breakdown products of degenerate germinal elements. 12M, 5/7, X67.
- FIG. 10. Testis of a two and one-half-year infantile bear during the postbreeding period. Seminiferous tubules are shrunken, basement membranes thickened and wrinkled, and the density of the central cytoplasmic complex increased. Interstitial tissue is relatively more abundant than during the breeding season with an increased cytoplasmic-nuclear ratio. Cf. Plate II, figure 8. 47N, 10/22, X32.
- FIG. 11. Postseasonal retrogression of the two and one-half-year infantile epididymis. Epididymis is nonfunctional, stereocilia are lost, and ducts reduced in size and surrounded by a thick, fibrous connective tissue coat. Most ducts are empty except for a heavy coagulum. Cf. Plate II, figure 9. 52N, 10/29, X30.
- FIG. 12. Testis of the prepuberal bear during the breeding season. Seminiferous tubules are markedly swollen and have a large lumen. Interstitial cells are sparse, confined to interstices between the tubules, and have a slightly higher cytoplasmic-nuclear ratio than in the spring infantile bear. 21M, 5/22, X27.
- FIG. 13. High power showing spermatogenic activity becoming arrested in the spermatocyte and spermatid stages in the prepuberal bear. The formation of multi-nucleated giant cells is a common feature. 21M, 5/22, X67.
- FIG. 14. High power showing greater cytoplasmic-nuclear ratio of the interstitial tissue of the spring prepuberal bear as compared to the infantile bear. Cf. Plate II, figures 2 and 3. 21M, 5/22, X67.
- FIG. 15. Immature and abnormal germ elements shed to the epididymis of the spring prepuberal bear. Most of the cells disintegrate in situ relatively few being passed to the epididymis and even fewer to the vas deferens. 21M, 5/22, X67.

PLATE IV

- FIG. 16. Prepuberal vas deferens showing limited numbers of immature and abnormal germ cells and the bleb-like secretions at the tips of the stereocilia. 21M, 5/22, X38.
- FIG. 17. Vas deferens of the prepuberal bear showing degenerate germ elements, including several spermheads, and highly active stereo-ciliated cells with abundant basally located presumed steroid products. 59M, 5/11, X67.
- FIG. 18. Declining spermatogenic activity in the postseasonal prepuberal bear. The tubules are reduced in diameter, the basement membranes thickened and wrinkled, and the germinal epithelium and lumina reduced. Note the occurrence of lymphocytes in the upper right tubule. 62A, 10/4, X67.
- FIG. 19. Continued testicular decline in the fall prepuberal bear. The lumina of the seminiferous tubules are reduced markedly and Sertoli cells predominate over the germinal forms. Interstitial tissue is more prominent than in the spring bear (Plate III, fig. 13). The cells are arranged in strands and have an increased cytoplasmic-nuclear ratio. Note the accumulation of lymphocytes at the lower margin of the upper left tubule. 73M, 10/14, X67.
- FIG. 20. Seminiferous tubules showing complete loss of spermatogenic elements in the postseasonal prepuberal bear. Note also the difference in activity state between various tubules within a given testis (Pl. IV, fig. 18). 62A, 10/4, X67.
- FIG. 21. Declining epididymis in the fall prepuberal bear. Epididymal ducts are becoming reduced in diameter and are being enveloped by a thick, fibrous, connective tissue coat. 62A, 10/4, X27.

PLATE V

- FIG. 22. Epididymis of the late fall prepuberal bear retaining a functional state beyond that of the vas deferens (Pl. V, fig. 23). Note the coagulum in the ducts. 9M, 10/10, X67.
- FIG. 23. Declining vas deferens in the late fall prepuberal bear. The decline precedes that of the epididymis (Pl. V, fig. 22) and is marked by a reduced duct diameter, and disorganization of the epithelium. 9M, 10/10, X30.
- FIG. 24. The prepuberal vas deferens in late decline. Duct epithelium is reduced to a single layer of low cuboidal cells. The duct contents are degradation products and a few abnormal cells. The ducts are surrounded by a thick, fibrous, connective tissue coat. Note that the decline of this organ precedes that of the seminiferous tubules (Pl. IV, fig. 19). 73M, 10/14, X38.
- FIG. 25. A presumed first-year adult showing spermatogenic activity in excess of that noted for the prepuberal bear (Pl. III, fig. 13) and with more abundant interstitial tissue. 22M, 4/22, X67.
- FIG. 26. Epididymis of presumed first-year adult showing a relatively large number of germinal elements, including a number of sperm heads. This condition parallels that of the fully mature bear at the approach of the breeding season when abnormal forms predominate. 22M, 4/22, X74.
- FIG. 27. Spermatogenic activity in the adult bear early in the breeding season. The tubules are rounded without distinct tubule lining and are not markedly swollen as they are later in the season. 42M, 4/18, X34.

PLATE VI

- FIGS. 28 & 29. Differing states of spermatogenesis between tubules. Interstitial tissue is abundant, loose, and stringy with a high cytoplasmic-nuclear ratio. The large size of the vacuoles within the cytoplasm is remarkable. 42M, 4/18, X67.
- FIG. 30. Multinucleated giant cells commonly observed in the redeveloping and declining adult testis, and in the prepuberal and two-year infantile testis. 6M, 5/15, X67.
- FIG. 31. Well-developed state of the epididymis of the early redeveloping bear. The sperm load is light and abnormal forms are common. 42M, 4/18, X67.
- FIG. 32. Redeveloping bear epididymis. Abundant accumulations of material among the stereocilia is a common feature. 1M, 5/4, X67.
- FIG. 33. Vas deferens of the redeveloping bear showing early sperm load containing large numbers of immature and abnormal germinal elements. 42M, 4/18, X42.

PLATE VII

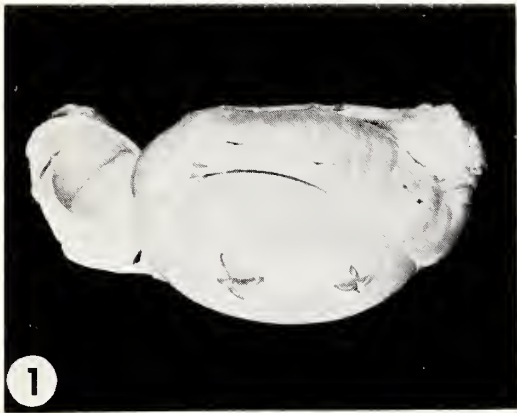
- FIG. 34. Testis of the fully active animal. The seminiferous tubules are markedly swollen and compressed together, with distinct lumina and all stages of spermatogenesis. Abnormal elements are rare. Interstitial cells are sparse and exhibit a relatively low cytoplasmic-nuclear ratio. 27M, 5/20, X54.
- FIG. 35. Epididymis at the height of the breeding season containing a heavy sperm load practically free of immature and abnormal forms. 1396, 5/12, X67.
- FIG. 36. Vas deferens at the height of the breeding season. The heavy sperm load suggests that the vas deferens is an important organ for sperm storage in this species. 17M, 5/23, X67.
- FIG. 37. Early spermatogenic decline in the adult bear. Spermatogenesis is becoming arrested in the spermatocyte and spermatid stages and abnormal forms are increasing. Interstitial cells are more abundant than during the breeding season and have larger amounts of cytoplasm (Pl. VII, fig. 34). However, the cytoplasmic-nuclear ratio is less than in the redeveloping testis (Pl. VI, figs. 28 and 29). 54N, 11/10, X89.
- FIG. 38. Degeneration of the germinal epithelium in the declining adult bear is accompanied by tubule shrinkage, thickening of the basement membranes, and the appearance of intertubular spaces. 54N, 11/10, X67.
- FIG. 39. Early declining testis showing reduction of the germinal epithelium and the peculiar and marked extension of the interstitial tissue into the tunica albuginea. 1820, 7/17, X27.

PLATE VIII

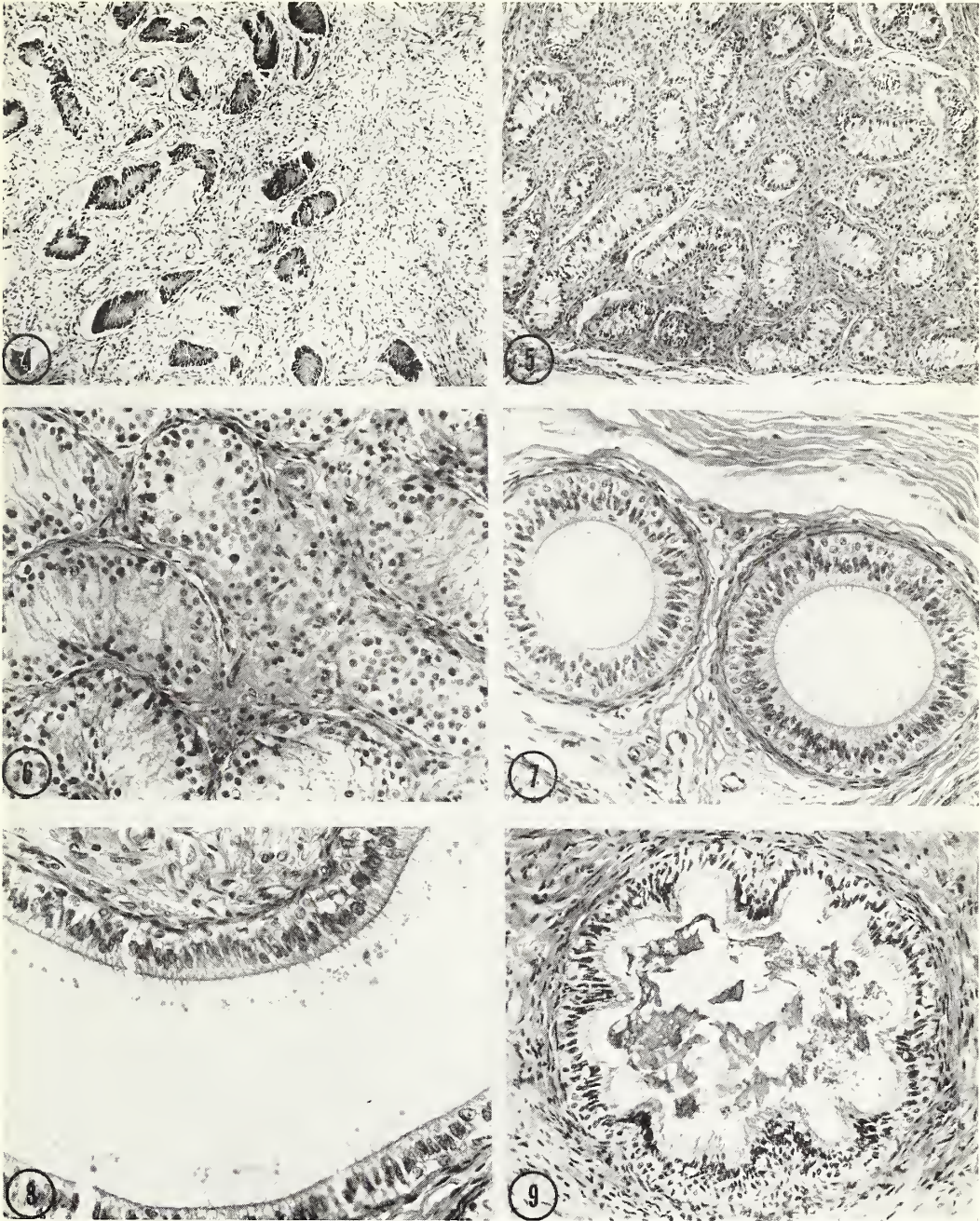
- FIG. 40. Further defoliation of the spermatogenic epithelium of the declining bear. Note particularly the formation of multinucleated giant cells probably by the coalescence of developing germ cells. 1820, 7/17, X67.
- FIG. 41. Complete loss of spermatogenic elements in individual tubules of the declining bear. 1831, 7/21, X30.
- FIG. 42. High magnification showing that the remaining cell population is Sertoli cells. 1831, 7/21, X67.
- FIG. 43. Marked germ cell degeneration affecting a whole tubule while spermatogenesis is still evident in adjacent tubules. 1831, 7/21, X30.
- FIG. 44. Apparently functional epididymis in a bear with marked spermatogenic decline (Pl. VII, fig. 37). The epididymal ducts are largely empty except for limited abnormal forms, secretory products, and coagulum. 54N, 11/10, X27.
- FIG. 45. Epididymis of the declining bear. The germinal elements are largely abnormal, the duct diameter reduced, and the epithelium disorganized. Heavy lymphocyte invasion (left) is general. 55N, 11/10, X67.

PLATE IX

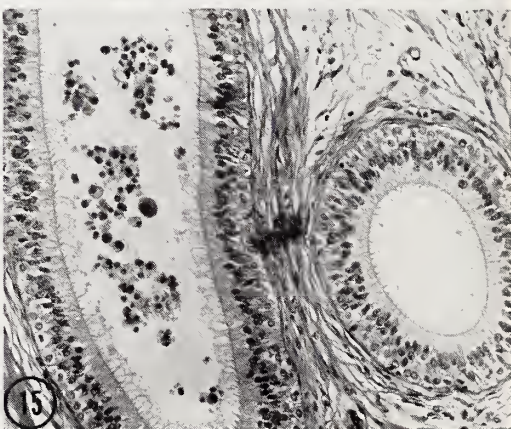
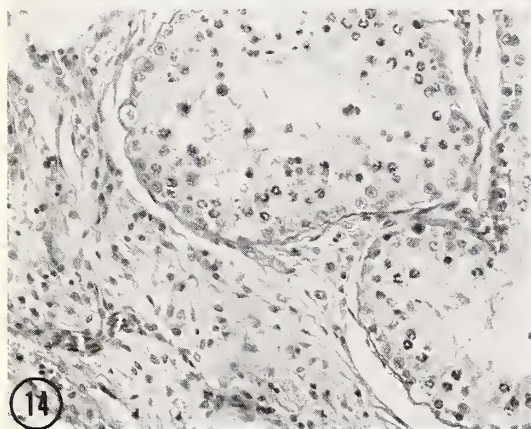
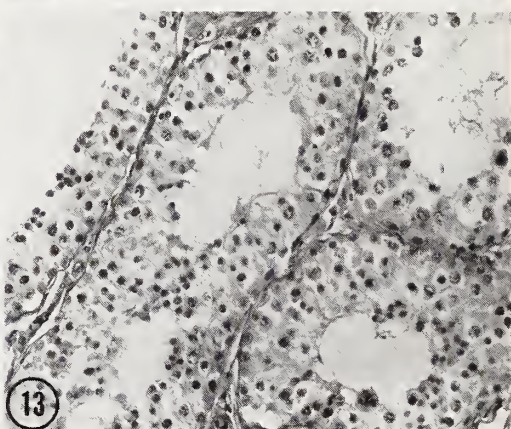
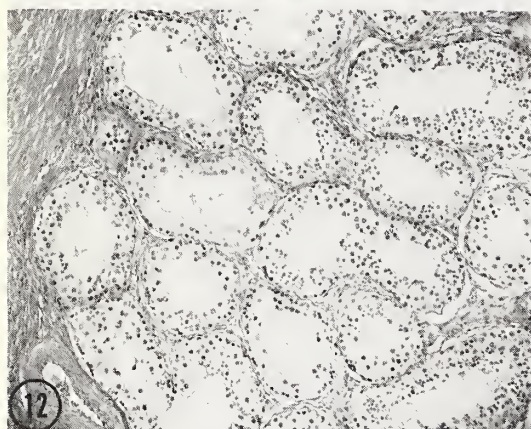
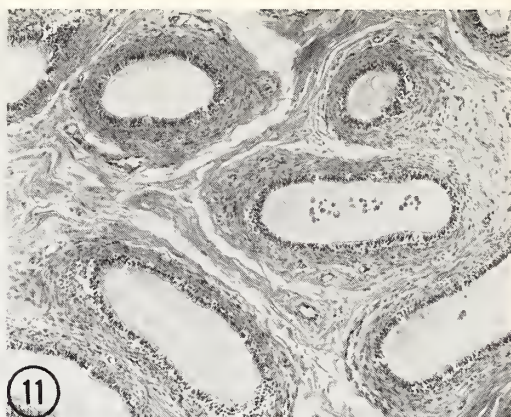
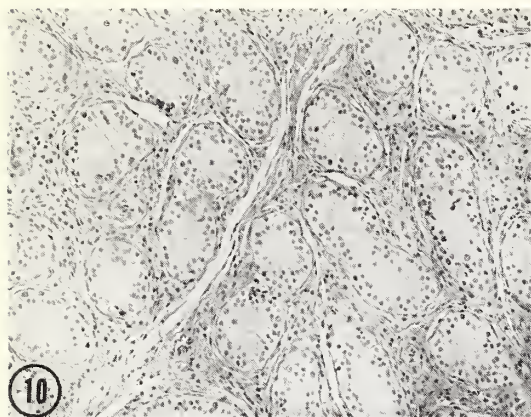
- FIG. 46. Declining bear showing epididymis largely free of germinal elements but with abundant coagulum the source of which is liquefaction of secretion products and degenerate germinal cell forms. 54N, 11/10, X67.
- FIG. 47. Vas deferens of the declining bear just prior to the major degenerative change (Pl. IX, fig. 48). 54N, 11/10, X34.
- FIG. 48. Atrophic vas deferens in the postseasonal bear. The epithelium is reduced to a single layer of low cuboidal cells, and the ducts are markedly reduced and surrounded by a thick, dense, connective tissue coat. Duct contents are largely debris and a few abnormal germ cells. 55N, 11/10, X34.
- FIG. 49. Epididymis of the late postseasonal bear. The ducts are reduced in diameter and surrounded by a heavy connective tissue coat. 55N, 11/10, X27.
- FIG. 50. Brown bear epididymal sperm typically retain a midpiece cytoplasmic droplet. Sperm washed from 10 percent formalin-fixed testis tissue and postfixed in O_8O_4 . Overall length of sperm is $78.2\ \mu$. E-305, 5/11.
- FIG. 51. A portion of the very profuse rete testis of the brown bear (Pl. I, fig. 3). The epithelium is typically a single layer of low cuboidal cells. 62A, 10/4, X84.



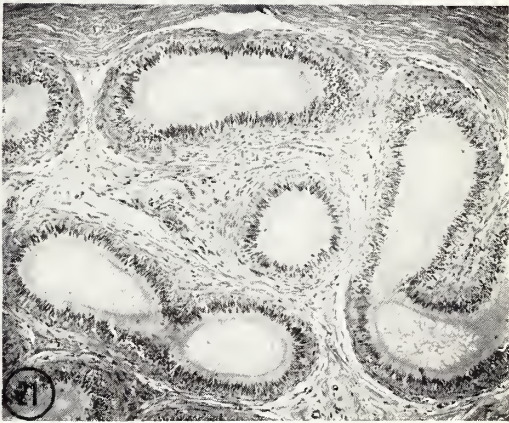
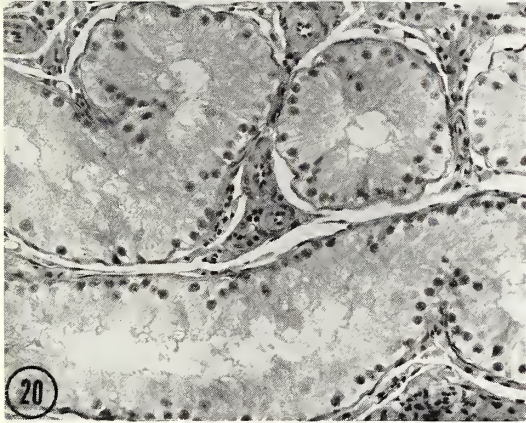
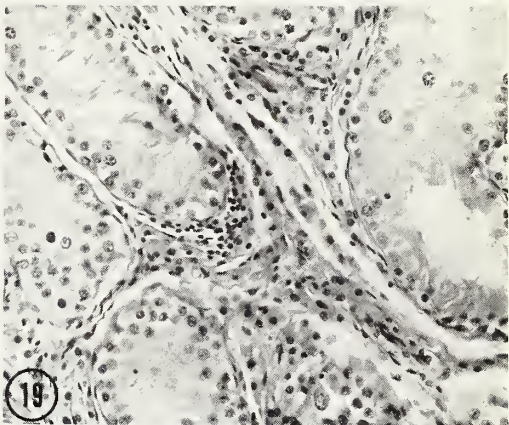
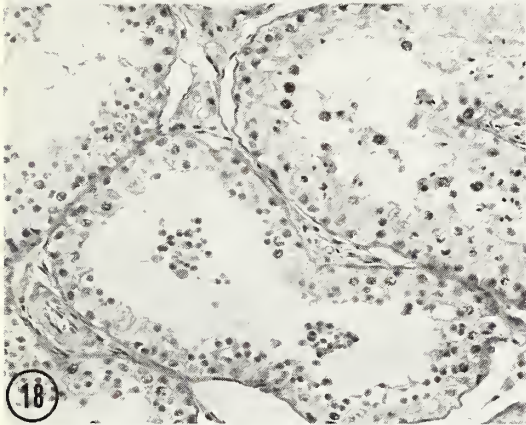
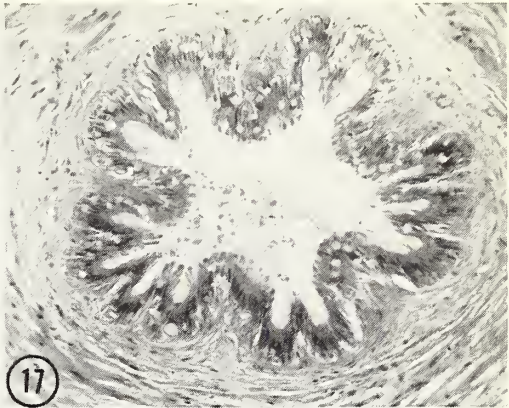
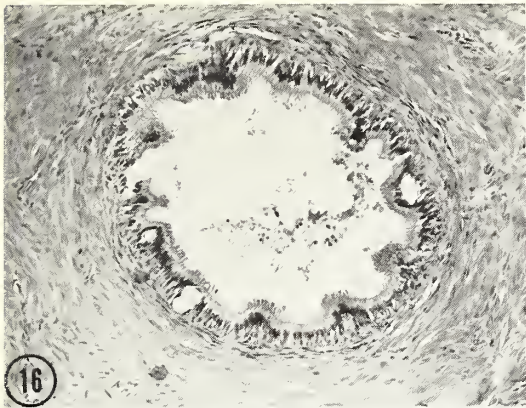
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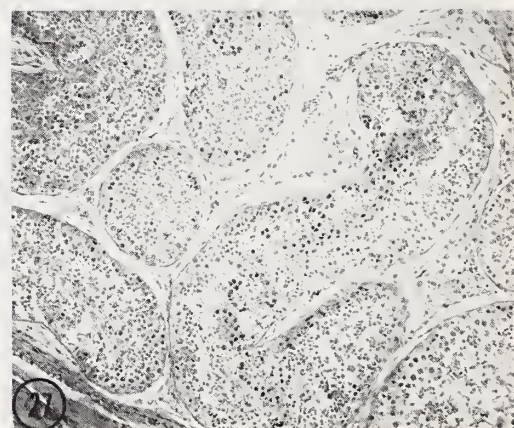
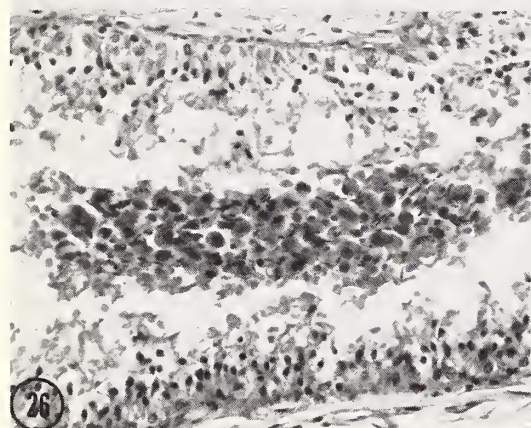
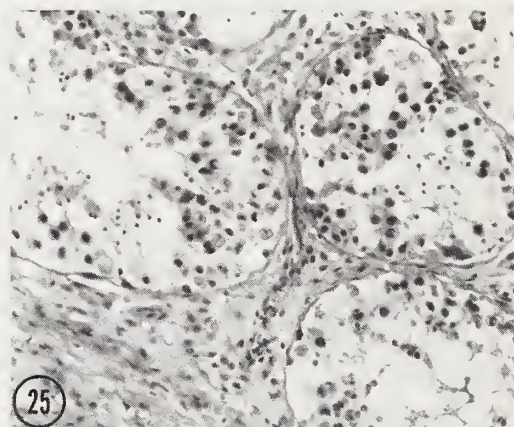
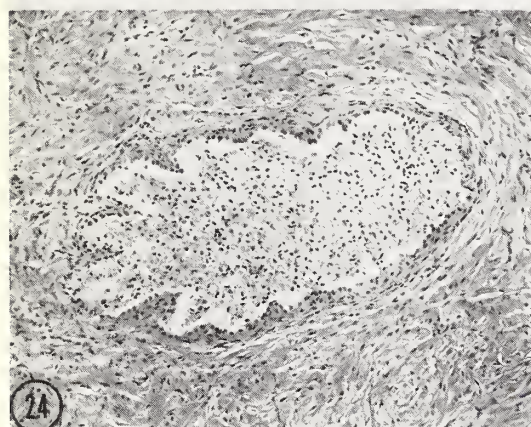
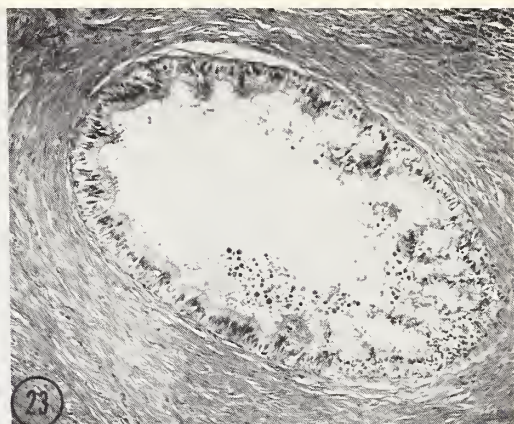
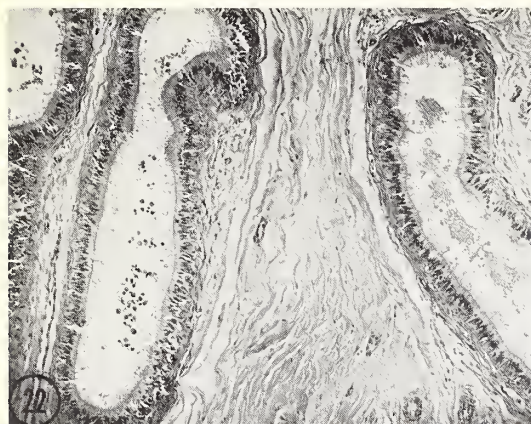
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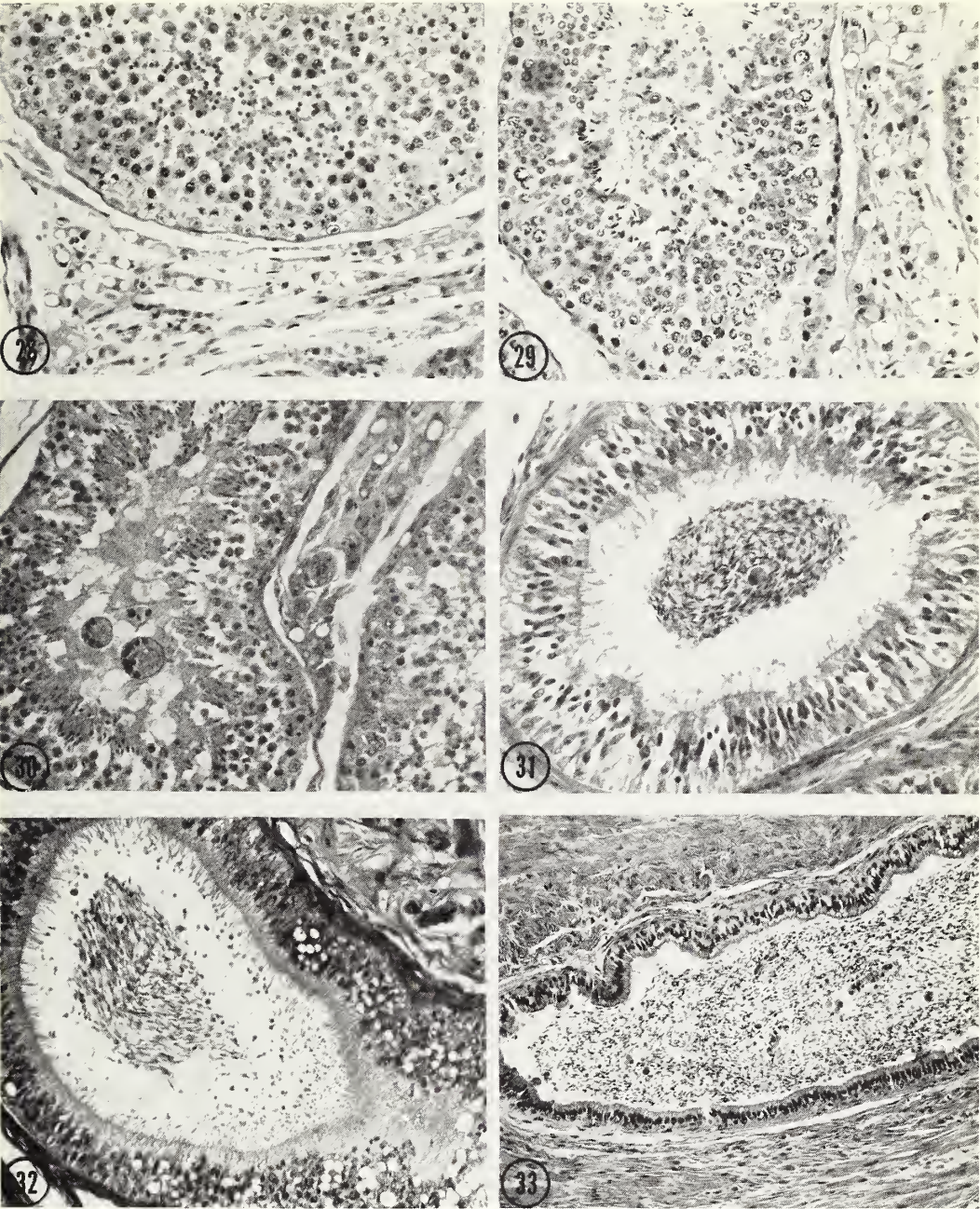
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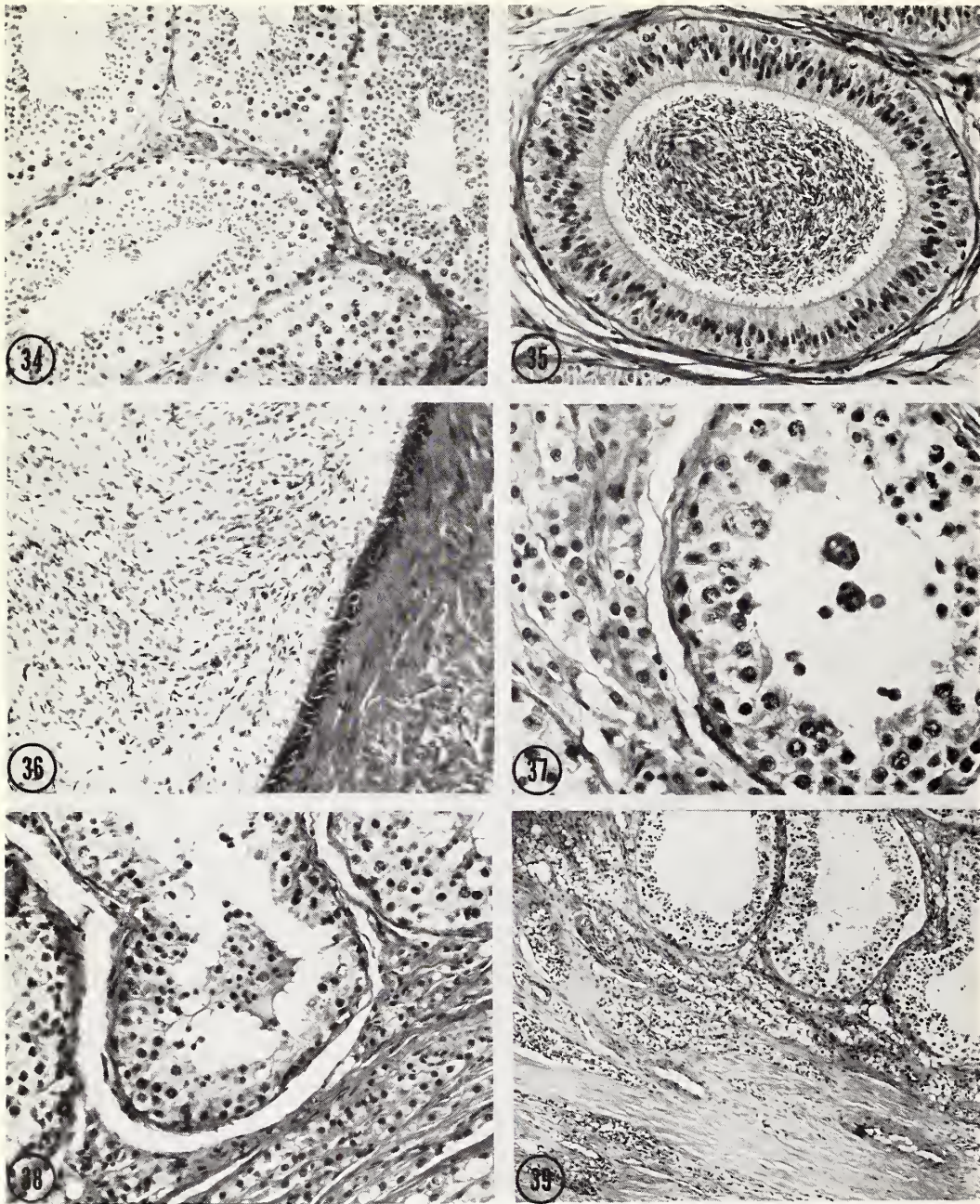
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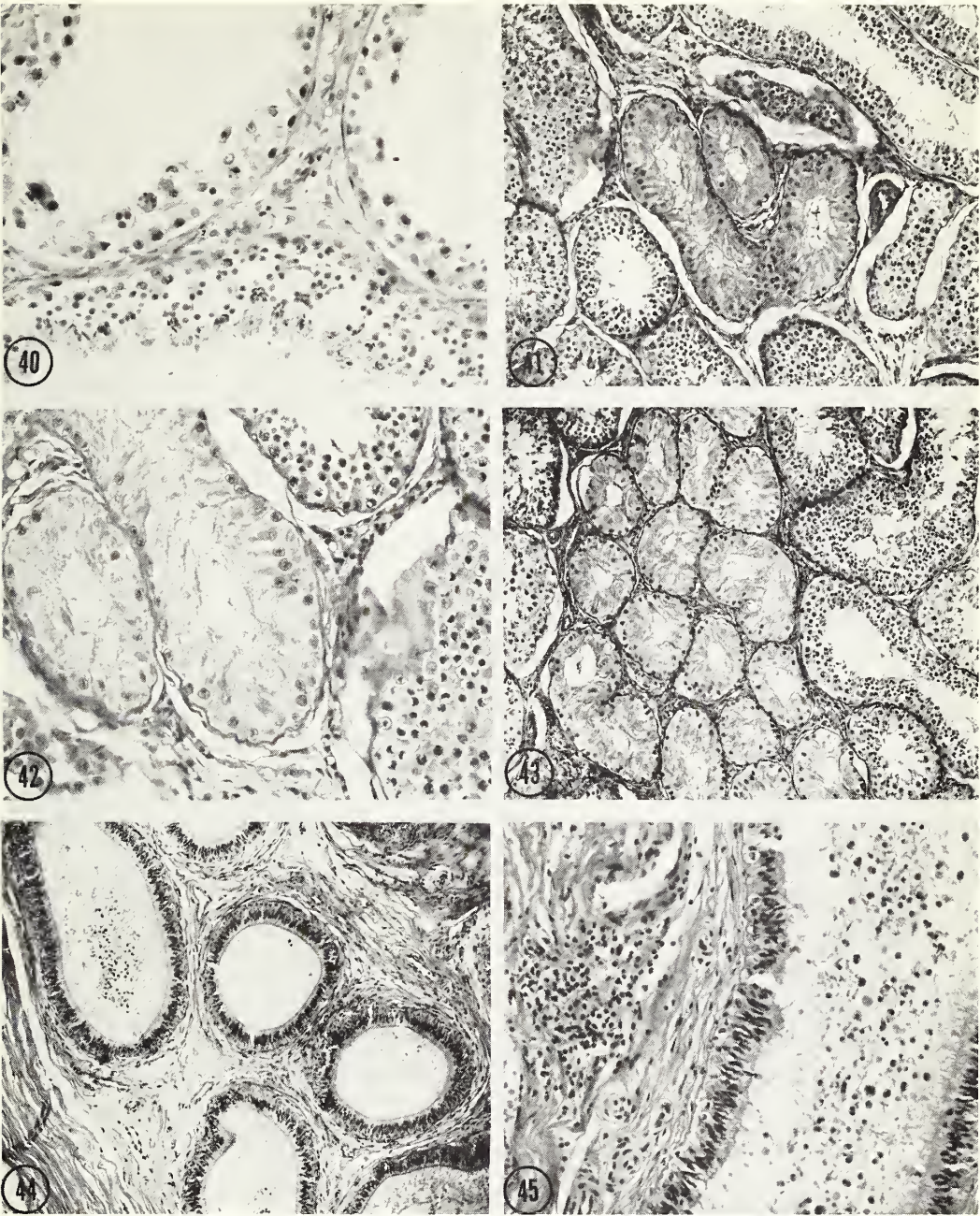
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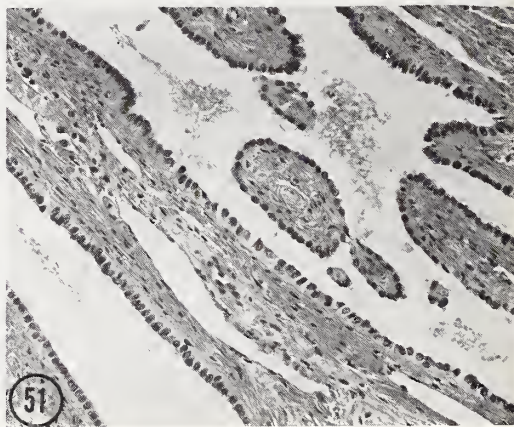
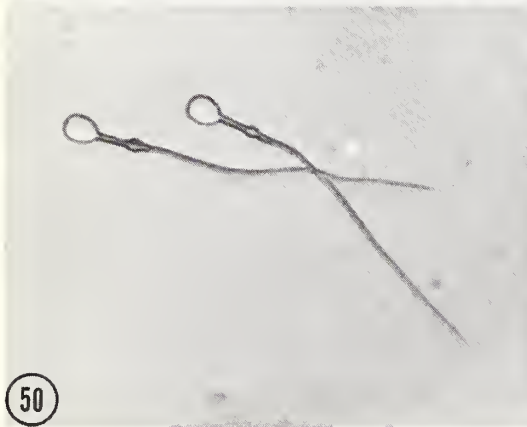
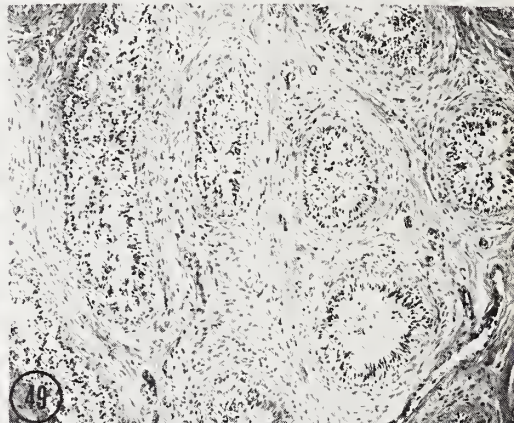
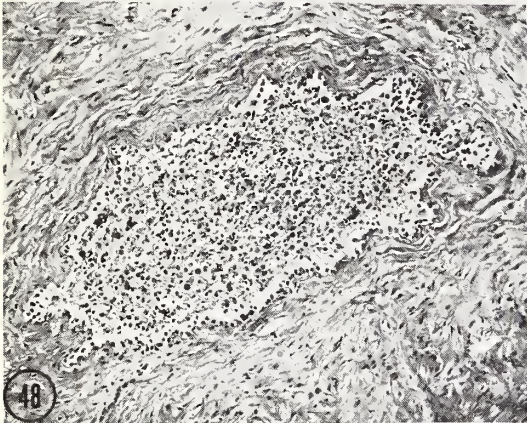
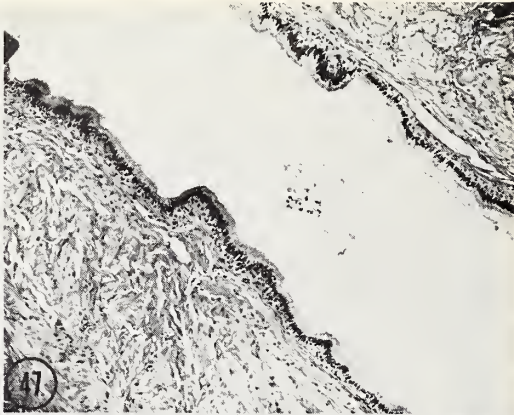
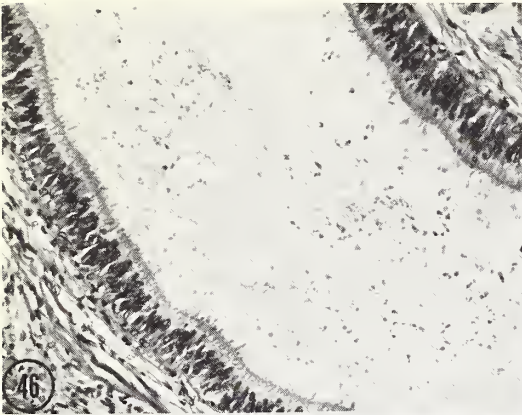
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THE BREEDING BIOLOGY OF THE MALE BROWN BEAR (*URSUS ARCTOS*)

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Host and Ecological Relationships of the Parasitic Helminth *Capillaria hepatica* in Florida Mammals

JAMES N. LAYNE¹

(Plate I; Text-figures 1-4)

INTRODUCTION

THE NEMATODE *Capillaria hepatica* (Bancroft, 1893) typically occurs as an adult in the liver of mammals, although in rare instances adult worms may be found in extra-hepatic sites. *Capillaria hepatica* is nearly cosmopolitan in its geographic distribution and exhibits broad host tolerance. Although rodents are the principal hosts, the parasite has been found in a number of species in other orders, including Primates, Lagomorpha, Carnivora, and Artiodactyla. Both genuine and spurious human infections have been reported (Ewing & Tilden, 1956; Lubinsky, 1956; MacArthur, 1924; McQuown, 1950, 1954; Otto *et al.*, 1954).

Although *C. hepatica* has been recorded from numerous hosts and localities in North America (Table 1), little is known about its status in populations of particular species or in different habitats or geographic regions. The most comprehensive data presently available on its incidence in natural populations of North American mammals are those of Freeman & Wright (1960) for several species of rodents in Algonquin Park, Ontario, Canada, and Layne & Griffo (1961) for the Florida mouse, *Peromyscus floridanus*. This paper presents additional information on the hosts, geographic and ecologic distribution, and incidence of *C. hepatica* in Florida.

METHODS AND MATERIALS

A total of 2,524 specimens of 27 species of mammals was examined. For the sake of completeness, the sample of *Peromyscus floridanus* reported on previously (Layne & Griffo, 1961) is included in the present analysis.

The majority of the animals was collected by live trapping and killed with ether for examination. Traps were generally set in lines with one or two traps per station and intervals of 30 to 50 ft. between stations, although in some instances traps were set in a 50 or 100 ft. grid. The remaining specimens were obtained by snap or steel trapping, shooting, or as road kills. Data recorded for each specimen usually included locality, date of collection, habitat, sex, age, body weight, external measurements, and reproductive condition.

Occurrence of an infection was based primarily on gross examination of the liver for the characteristic lesions of *C. hepatica* (Pl. I, fig. 1). According to Freeman & Wright (1960), infections of two or more weeks duration should be reliably detected by this method. A further indication of its validity is the fact that use of a formalin-ether concentration technique in the previous study (Layne & Griffo, 1961) did not reveal any infections that had been overlooked during routine autopsy. In the relatively few instances where there was some doubt as to the nature of a lesion, portions of tissue from the area in question were teased apart in a drop of water on a microslide, compressed with a cover slip, and scanned at 100X for the presence of ova (Pl. I, figs. 2 and 3) or fragments of adult worms.

¹Archbold Biological Station, Lake Placid, Florida 33852 and Department of Mammalogy, The American Museum of Natural History, New York, N.Y. 10024.

TABLE I

SUMMARY OF NORTH AMERICAN HOST AND LOCALITY RECORDS FOR *Capillaria hepatica*

Host	Locality and Authority
Order Primates	
<i>Ateles geoffroyi</i>	Mexico: Chiapas (Caballero & Grocott, 1952); Panama (Foster & Johnson, 1939)
<i>Cebus capucinus</i>	Panama (Foster & Johnson, 1939)
Order Carnivora	
<i>Canis familiaris</i>	U.S.:? Washington, D. C. and vicinity (Wright, 1930)
Order Lagomorpha	
<i>Sylvilagus floridanus</i>	U.S.: Oklahoma (Ward, 1934)
Order Rodentia	
<i>Marmota monax</i>	U.S.: Pennsylvania—zoo specimen (Doran, 1955)
<i>Cynomys ludovicianus</i>	U.S.: Pennsylvania—zoo specimen (Weidman, 1925)
<i>Citellus richardsonii</i>	Canada: Alberta (Brown & Roy, 1943); U.S.: Montana (Luttermoser, 1938)
<i>Sciurus niger</i>	U.S.: Louisiana (McQuown, 1954)
<i>Castor canadensis</i>	U.S.: Washington, D. C.—zoo specimen (Chitwood, 1934)
<i>Thomomys talpoides</i>	Canada: Alberta (Lubinsky, 1956, 1957); U.S.: Wyoming (Dikmans, 1932; Law & Kennedy, 1932—cited from Lubinsky, 1956; Rausch, 1961)
<i>Geomys bursarius</i>	U.S.: Pennsylvania—zoo specimen (Weidman, 1917)
<i>Neotoma cinerea</i>	U.S.: Oregon (Rausch, 1961)
<i>Peromyscus floridanus</i>	U.S.: Florida (Layne & Griffo, 1961; Layne, 1963; present study)
<i>Peromyscus gossypinus</i>	U.S.: Florida (present study)
<i>Peromyscus maniculatus</i>	Canada: Alberta (Lubinsky, 1956, 1957); Ontario (Freeman, 1958; Freeman & Wright, 1960); U.S.: Alaska (Rausch, 1961); New York (Layne, unpublished);? Washington (Dalquest, 1948); artificial infection, species uncertain (Luttermoser, 1938)
<i>Sigmodon hispidus</i>	U.S.: Florida (present study); Texas (Read, 1949)
<i>Clethrionomys gapperi</i>	Canada: Ontario (Freeman & Wright, 1960); U.S.: New York (Fisher, 1963)
<i>Microtus chrotorrhinus</i>	U.S.: New York (Fisher, 1963)
<i>Microtus pennsylvanicus</i>	Canada: Ontario (Freeman & Wright, 1960)
<i>Synaptomys cooperi</i>	Canada: Ontario (Freeman & Wright, 1960)
<i>Lemmus sibiricus</i>	U.S.: Alaska (Rausch, 1961)
<i>Ondatra zibethicus</i>	Canada: Ontario (Freeman & Wright, 1960); Ontario—fur farm (Law & Kennedy, 1932—cited from Lubinsky, 1956; Price, 1931; Swales, 1933); U.S.: Louisiana (Penn, 1942); Maine (Meyer & Reilly, 1950); Michigan (Ameel, 1942)
<i>Mus musculus</i>	U.S.: Maryland (Luttermoser, 1938); Pennsylvania (Doran, 1955)
<i>Rattus rattus</i>	Panama (Calero <i>et al.</i> , 1950); U.S.: (Hall, 1916)
<i>Rattus norvegicus</i>	Canada: Quebec (Firlotte, 1948); Panama (Calero <i>et al.</i> , 1950) U.S.: Illinois (Wantland <i>et al.</i> , 1956); Maryland (Calhoun, 1962; Davis, 1951; Habermann <i>et al.</i> , 1954; Luttermoser, 1936; Shorb, 1931; Yokogawa, 1920); New York (Herman, 1939); North Carolina (Harkema, 1936); Pennsylvania (Herman, 1939); Washington, D. C. (Cram, 1928; Price & Chitwood, 1931).
<i>Rattus rattus</i> or <i>R. norvegicus</i>	U.S.: California;? Pennsylvania; Rhode Island; Washington, D.C. (Hall, 1916)
<i>Napaeozapus insignis</i>	Canada: Ontario (Freeman & Wright, 1960)
Order Artiodactyla	
<i>Tayassu pecari</i>	Panama (Foster & Johnson, 1939)
<i>Sus scrofa</i>	U.S.: domestic—artificial infection (Tromba, 1959)

Infections were rated as to severity on the basis of the appearance and abundance of lesions. Luttermoser (1938) considered the extent of lesions rather than actual egg counts to be better as an index of degree of infection. Cases in which the liver had small, discrete, and widely scattered lesions, often confined to a single lobe, were regarded as light. Infections in which the lesions were more numerous and extensively distributed were classified as moderate, whereas those in which the lesions were almost continuous and involved most or all of the hepatic lobes were rated as heavy.

Collections were made in 22 counties of the state, with emphasis on the north-central region. An attempt was made to sample as wide a range of habitats as possible. Although specimens were taken only casually (e.g. as road kills) in some habitat types, over 20 distinct vegetative types were systematically live trapped or snap trapped for small rodents. For present purposes these may be grouped under nine major categories which are briefly described below. More detailed descriptions of most of these may be found in Carr (1940), Laessle (1942, 1958), and Rogers (1933). Rogers (1933) and Cooper *et al.* (1959) also give data on air and soil temperatures and evaporation rates for some of the habitats included here.

1. *Hammocks*. Mixed hardwood forests, including mesophytic, upland, live oak, and cabbage palm hammocks. The first of these has laurel oak (*Quercus laurifolia*), magnolia (*Magnolia grandiflora*), and American holly (*Ilex opaca*) as characteristic tree species. The soils are rich in organic matter and usually moist. Upland hammocks are drier than the preceding, with laurel oak, southern red oak (*Q. falcata*), persimmon (*Diospyros virginiana*), mockernut hickory (*Carya tomentosa*), and loblolly pine (*Pinus taeda*) being representative tree species. Live oak hammocks, with live oak (*Q. virginiana*) as the dominant tree and generally sparse ground cover, are also comparatively xeric. Cabbage palm hammocks sampled consisted of dense stands of cabbage palm (*Sabal palmetto*) and other trees and shrubs. Soils were rich and moist.

2. *Pine-oak woodlands*. Generally open stands of pines and oaks occurring on sandy well-drained soils, often on low ridges or hills. Ground cover is generally rather sparse resulting in frequent patches of exposed sand. Two types of pine-oak woodlands were sampled in the study, one with longleaf pine (*Pinus palustris*) and turkey oak (*Q. laevis*) as the chief tree species, and the other with slash pine (*P. elliotii*) and turkey oak. The first is widespread through-

out much of Florida, while the second is restricted to a relatively small area in the south-central part of the peninsula. Slash pine-turkey oak woodlands are somewhat intermediate between longleaf pine-turkey oak woodlands and sand pine scrub, described below, in over-all species composition and environmental conditions. Only one of 18 different pine-oak woodland habitats from which collections were made represented slash pine-turkey oak.

3. *Scrub*. Stands of scattered pines with a dense understory of small trees and shrubs, a number of which are sclerophyllous. Herbaceous ground cover is typically sparse, and open sandy patches are common. This comparatively xeric vegetative type occurs on excessively well-drained fine sandy soils. Sand pine (*P. clausa*) is generally regarded as the most characteristic species of true scrub, and myrtle oak (*Q. myrtifolia*), live oak, and Chapman oak (*Q. chapmanii*) are the principal elements of the shrub layer. For purposes of the present study, one station (Levy-19) with all of the characteristics of scrub except for slash instead of sand pine is included under this category.

4. *Flatwoods*. Level pinelands found on poorly drained soils. The particular species of pine present as the dominant tree depends upon edaphic conditions. Longleaf pine is typical of better drained sites and slash pine of the more moist areas. Ground cover in flatwoods is usually dense, consisting of varying proportions of grasses, palmettos, and forbs. Shrubs and deciduous trees range from rare to abundant enough to form a distinct understory, depending on frequency of fire.

5. *Swamps*. Cypress (*Taxodium distichum*) and hardwood swamps and bayheads. The latter are low, moist to wet, dense stands of various trees, shrubs, and vines. Sweetbay (*Magnolia virginiana*) and loblolly bay (*Gordonia lasianthus*) are common species of bayheads.

6. *Wetlands*. Moist to wet prairies, marshes, and lush herbaceous and brushy borders of roadside ditches and ponds.

7. *Dunes*. Coastal sand dunes generally sparsely vegetated with sea oats (*Uniola paniculata*) and various other grasses and forbs.

8. *Ruderal*. Old fields in early successional stages, pine plantations, weedy or grassy road shoulders, and fence rows.

9. *Miscellaneous*. Buildings and lawns or gardens in agricultural or residential areas. Except for snap trapping for *Mus musculus* and *Rattus*, no systematic collecting was carried out in these habitats.

Although in many cases a given locality was sampled only once, periodic trapping of selected

TABLE II
SPECIES AND NUMBERS OF FLORIDA MAMMALS EXAMINED FOR *Capillaria hepatica*
Asterisk Indicates Habitat or Locality from which Infections were Recorded

Species	No. exam.	Habitat ¹	Locality ²
<i>Didelphis marsupialis</i>	6	H1, P1, S1, U3	A3, H1, Lv1, U1
<i>Scalopus aquaticus</i>	5	P1, M2, U2	A4, La1
<i>Cryptotis parva</i>	10	P1, F6, W1, R2	A10
<i>Blarina brevicauda</i>	6	H3, W3	A5, H1
<i>Sylvilagus floridanus</i>	12	H7, S1, F1, R2, U1	A3, B1, H7, Le1
<i>S. palustris</i>	4	W3, R1	A1, Lv1, Pi2
<i>Sciurus carolinensis</i>	11	H4, M2, U5	A8, H1, Lv1, Pi1
<i>S. niger</i>	2	P1, F1	A1, Lv1
<i>Glaucomys volans</i>	2	R1, M1	A2
<i>Geomys pinetis</i>	9	P3, S1, R4, U1	A1, G1, H2, Lv4, St1
<i>Oryzomys palustris</i>	32	S7, F5, W17, R2, M1	A7, H6, Le5, Lv13
<i>Peromyscus polionotus</i>	43	P3, S2, F1, D34, R3	A3, B3, E30, H6, O1
<i>P. gossypinus</i>	254	H39, P19, S126*, F9, Sw32*, W1, R1, U5	A55, B12, Fr7, H38, Lv141*, St1
<i>P. floridanus</i>	1312	H246*, P400*, S600*, F61, R16, U1	A634, C4, G18, H75*, Lv570*, Pa6, Pu1, St4*
<i>Reithrodontomys humulis</i>	2	P2	A2
<i>Ochrotomys nuttalli</i>	12	H3, P5, S4	A4, H2, Le2, St4
<i>Sigmodon hispidus</i>	427	H3, P32, S200*, F66, Sw18, W40, D9, R51*, U8	A123, B4, E6, H36*, Le11, Lv213, Pi27, St6, W1
<i>Neotoma floridana</i>	2	H1, S1	Lv1, T1
<i>Neofiber alleni</i>	9	W9	A3, H5, Pu1
<i>Rattus norvegicus</i>	1	M1	Dw1
<i>Rattus rattus</i>	18	R4, M11, U3	A2, Du2, M2, Pi12
<i>Mus musculus</i>	328	H7, P1, S3, W13, D3, R2, M297, U2	A303, H3, Le19, O3
<i>Urocyon cinereoargenteus</i>	6	H1, P1, U4	A3, F1, H1, Pu1
<i>Procyon lotor</i>	5	S1, R1, U3	A1, H1, Lv1, M2
<i>Mustela frenata</i>	1	U1	Du1
<i>Mephitis mephitis</i>	1	D1	De1
<i>Lynx rufus</i>	4	H1, R1, U2	A2, De1, T1

¹Habitat Key:

H—hammocks, P—pine-oak woodlands, S—scrub, F—flatwoods, Sw—swamps, W—wetlands, D—dunes, R—ruderal, M—miscellaneous, U—unknown. Number of specimens examined from given habitat type follows abbreviation.

²Locality (county) Key:

A—Alachua, B—Brevard, C—Clay, De—DeSoto, Du—Duval, E—Escambia, F—Flagler, Fr—Franklin, G—Gilchrist, H—Highlands, La—Lake, Le—Lee, Lv—Levy, M—Monroe, O—Okaloosa, Pa—Palm Beach, Pi—Pinellas, Pu—Putnam, Sa—Santa Rosa, St—St. Johns, T—Taylor, W—Walton, U—Unknown. Number of specimens examined from given county follows abbreviation.

pine-oak woodland, scrub, flatwoods, hammock, and ruderal habitat types was conducted in order to obtain data on seasonal and long-term trends in prevalence of *C. hepatica* in small mammal populations. The numbers of samples obtained from a given station ranged from two in a two-year period to 21 over an eight-year interval.

RESULTS

Host and geographic distribution. The species and numbers of mammals examined for *C. hepatica* and localities represented are listed in Table 2. Eight per cent of the 2,524 specimens and 11% (3) of the 27 species examined had *Capillaria* infections. The species and localities from which infections were recorded included the Florida mouse, *Peromyscus floridanus*, from Highlands, Levy, and St. Johns Counties; the cotton mouse, *Peromyscus gossypinus*, from Levy County; and the cotton rat, *Sigmodon hispidus*, from Highlands and Levy Counties. *C. hepatica* has not been previously reported from the cotton mouse, and *Sigmodon* constitutes a new host record for Florida and the southeastern United States generally.

Based on total numbers of specimens examined from all habitats combined, incidence of infection was 15.4% in *P. floridanus*, 6.3% in *P. gossypinus*, and 10.5% in *Sigmodon*. Because infection rates in populations in the same and different habitats varied considerably and sample sizes are unequal, these values probably do not reflect the true status of *C. hepatica* in these species as well as a mean incidence calculated from individual population means. Expressed in the latter manner, incidence was 13.2% in Florida mice, 2.5% in cotton mice, and 6.3% in cotton rats.

Considering only those localities from which infected animals of any species were collected (Table 3), prevalence of *C. hepatica* was 34.2% in Florida mice, 14.8% in cotton mice, and 21.1% in cotton rats. As there are significant differences in the probability of infection in different age groups, the above values may be influenced by different age compositions of the samples of each species. Thus incidence based only on adult animals is probably a more satisfactory value for comparative purposes. Adult infection rates in *P. floridanus*, *P. gossypinus*, and *Sigmodon* were 37.7%, 14.8% and 30.8%, respectively. Neither the total nor adult infection rates in *P. floridanus* and *Sigmodon* differ statistically when tested by chi-square ($P > .05$), but both species differ significantly from *P. gossypinus* ($P < .005$).

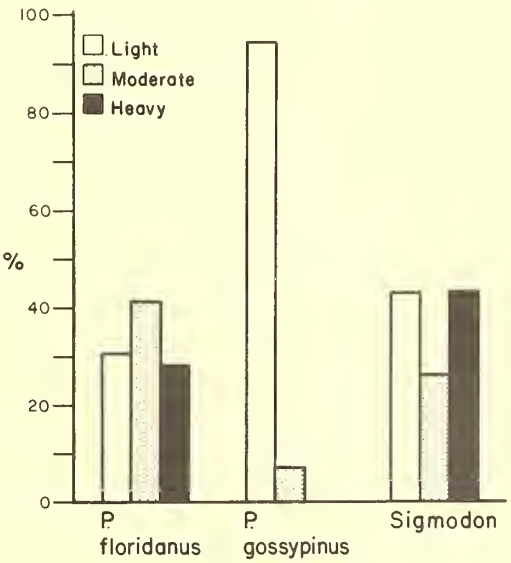
Florida mice and cotton rats tended to be more heavily infected than cotton mice (Text-

fig. 1). The difference in severity of infections between *P. gossypinus* and the other species is significant ($P < .05$), but *P. floridanus* and *Sigmodon* do not differ significantly in the proportions of light, moderate, and heavy infections.

With one exception, all infections of *C. hepatica* observed in this study were localized in the liver as is typical. However, one cotton rat with a massive early infection of the upper hepatic lobes also had scattered adult worms in the mesentery of the spleen and a "knot" of worms about ¼-inch in diameter in the mesentery adjacent to the liver. The worms at the latter site appeared to be dead and in the process of becoming calcified. No ova were observed when teased fragments of the worms were examined microscopically.

Infected livers of *P. floridanus* differed markedly in appearance from those of the other species. Even in the case of the lightest infections, the livers of Florida mice became prominently lobulated, contrasting greatly with the normally smooth surface of the organ (Pl. I, fig. 1). Although the liver of one heavily infected cotton rat had a slightly lobulated appearance, all other infected livers of *Sigmodon* and cotton mice were normal in appearance except for the presence of lesions.

Ecological distribution. Infected mice were recorded from five (hammocks, pine-oak woodlands, scrub, swamps, and ruderal) of the nine



TEXT-FIG. 1. Severity of infections of *C. hepatica* in three Florida rodent species.

TABLE III
INCIDENCE OF *Capillaria hepatica* INFECTIONS IN POPULATIONS OF THREE RODENT SPECIES

Habitat and Locality	<i>P. floridanus</i>						<i>P. gossypinus</i>						<i>Sigmodon</i>					
	Total			Adults			Total			Adults			Total			Adults		
	N	%	inf.	N	%	ex.	N	%	inf.	N	%	ex.	N	%	inf.	N	%	ex.
Scrub	19	7	36.8	18	7	38.9	6	0	0	6	0	0	16	0	0	16	0	0
Highlands-12																		
Levy-1	7	2	28.6	3	2	66.7	1	0	0	1	0	0	30	4	13.3	14	4	28.6
Levy-3	11	7	63.6	8	5	62.5	—	—	—	—	—	—	2	0	0	2	0	0
Levy-10	203	23	11.3	177	22	12.4	10	4	40.0	8	3	37.5	40	4	10.0	29	4	13.8
Levy-19*	213	126	59.2	178	116	65.2	70	12	17.1	55	12	21.8	86	32	37.2	50	27	54.0
Levy-28	82	30	36.6	76	29	38.2	22	0	0	22	0	0	17	3	17.6	6	3	50.0
St. Johns-23	1	1	100.0	1	1	100.0	—	—	—	—	—	—	—	—	—	—	—	—
St. Johns-24	1	1	100.0	1	1	100.0	—	—	—	—	—	—	—	—	—	—	—	—
Slash pine- turkey oak																		
Highlands-13	53	4	7.5	33	3	9.3	7	0	0	7	0	0	1	1	100.0	1	1	100.0
Ruderal (grassy)																		
Highlands	—	—	—	—	—	—	—	—	—	—	—	—	19	1	5.3	10	1	10.0
Hammock (live-oak)																		
St. Johns-24	1	1	100.0	1	1	100.0	—	—	—	—	—	—	—	—	—	—	—	—
Swamp (bayhead)																		
Levy-19	—	—	—	—	—	—	9	1	11.1	9	1	11.1	2	0	0	2	0	0

*Typical scrub vegetation but with slash instead of sand pine as noted in text.

major habitat categories sampled (Table 2). Including all mammals obtained from all habitats combined, over-all infection rates were 0.3% in hammocks, 1.1% in pine-oak woodlands, 26.0% in scrub, 2.0% in swamps, and 1.1% in ruderal situations. The data thus reveal a strong preponderance of infections in scrub habitats. This indication of habitat specificity in the occurrence of *C. hepatica* is further strengthened when the data are examined in greater detail. All non-scrub habitats from which infected animals were collected were located within dispersal distance of scrubs with moderate to high incidence of *C. hepatica*.

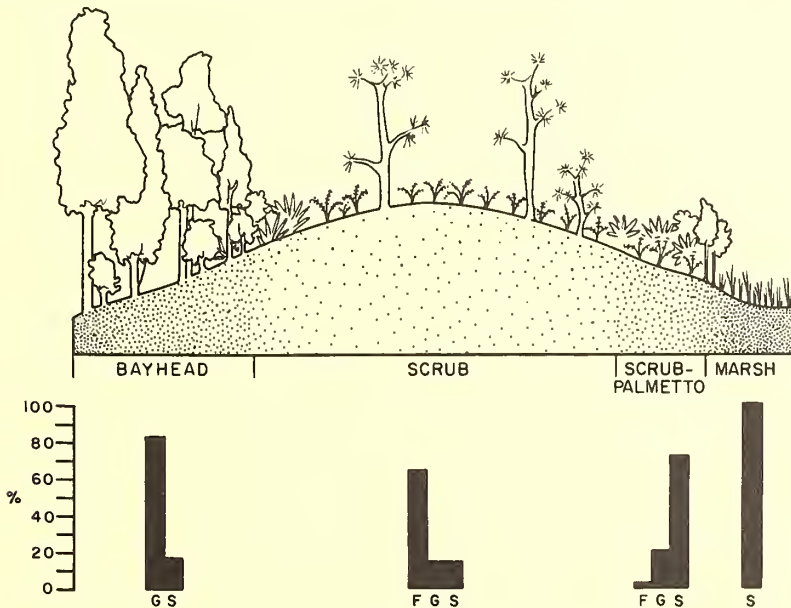
Data from a locality in Levy County (Levy-19) that was studied over an eight-year period provide a particularly clear example of the close correlation between the occurrence of *C. hepatica* and scrub environments. The scrub vegetation at this site was restricted to a slightly elevated area and graded abruptly into surrounding low bayhead and marsh habitats (Text-fig. 2). Of the 418 mammals examined from this area, 46% of those collected in the scrub were infected as compared to only 2% from the adjacent habitat types. It is also likely that the infected animals from the adjoining habitats had acquired their infections in the scrub.

Table 3 summarizes data on prevalence of *Capillaria* in the three rodent species at all stations in which infections occurred in at least

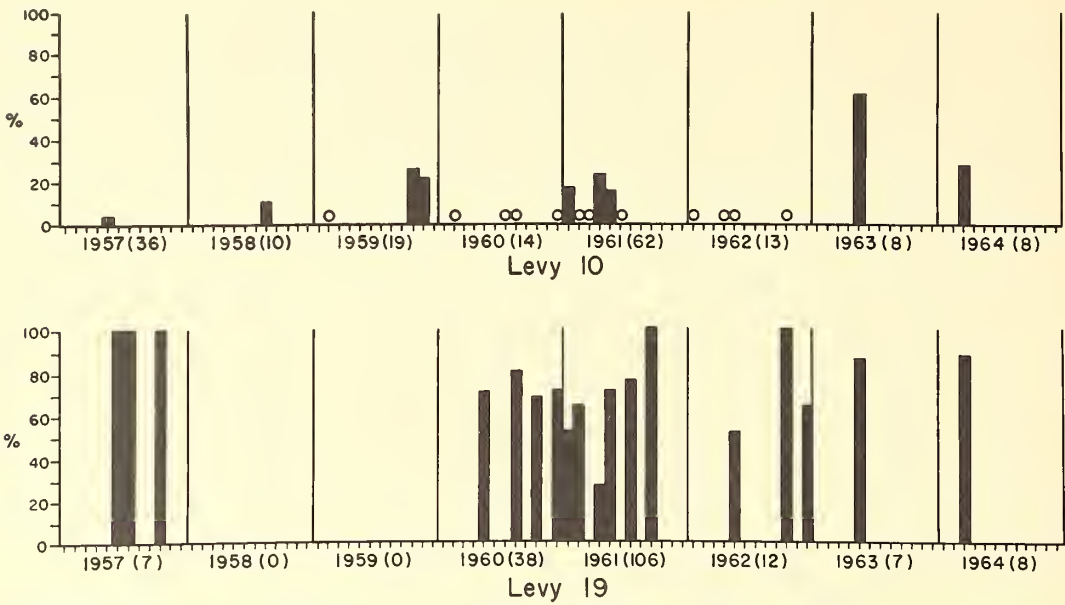
one of the species. The incidence of infections is strongly correlated with the extent to which a species occurs in scrub and its general abundance in this habitat. The data also indicate considerable intraspecific variation in infection rates within a given habitat type. Such variability tends to be greater in *Sigmodon* and *P. gossypinus* than in *P. floridanus*, with the last species also exhibiting consistently higher infection rates. There also appears to be some tendency in at least the Florida mouse and cotton rat for infection rates at different stations to vary in the same direction.

Geographic differences in infection rates in different species or populations of the same species are not apparent from the present data. There was as much variation in inter- and intra-specific infection rates between stations 1, 3, 10, 19, and 28 in Levy County, all of which are within 5 miles of one another, as between those in different parts of the state.

Multiple samples from the same station show yearly fluctuations in incidence of *Capillaria*. However, there is some evidence from two *P. floridanus* scrub populations sampled over an eight-year period that infection levels in a given population may vary within relatively narrow limits for a considerable span of time (Text-fig. 3). The two populations in question are located only about 5 miles apart, yet are separated by unsuitable habitat.



TEXT-FIG. 2. Relationships of habitats at station Levy-19 and host species composition in each. Corresponding data on infection rates given in text. Density of stippling indicates degree of soil moisture; vertical scale somewhat exaggerated. Symbols: F = *P. floridanus*, G = *P. gossypinus*, S = *Sigmodon hispidus*.



TEXT-FIG. 3. Prevalence of *C. hepatica* infections in adult *P. floridanus* in two nearby scrub habitats from 1957 to 1964. Samples examined each year are given in parentheses following year.

Sex and age differences in infections. Table 4 gives the sex and age distribution of *C. hepatica* in infected host populations. The age classes used for the two *Peromyscus* species are based on pelage features. Mice assigned to the juvenile age class were still in the full gray juvenile pelage and showed no sign of molt on the dorsum. Individuals undergoing the dorsal phase of the postjuvenile molt were regarded as subadults, while mice in which the postjuvenile molt had been completed were assigned to the adult class. Approximate chronological ages corresponding

to these pelage phases are under 6 weeks for juveniles, 6 to 13 weeks for subadults, and over 14 weeks for adults (Layne, 1966; Pournelle, 1952). Age classes of cotton rats were based on body weight as follows: juvenile, less than 40 g; subadult, 40-70 g; and adult, above 70 g. A relationship between age and infection rate is evidenced by all species. No parasitized juveniles were found in any species, although samples of this age class are admittedly small. Adult infection rates are significantly higher ($P < .05$) than those of subadults in both Florida

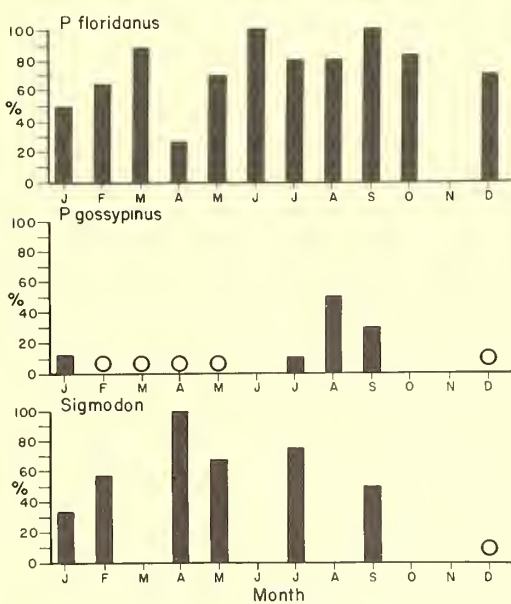
TABLE IV
SEX AND AGE DIFFERENCES IN *Capillaria hepatica* INFECTIONS

Species	Age class	Male			Female			Total		
		N ex.	N inf.	%	N ex.	N inf.	%	N ex.	N inf.	%
<i>P. floridanus</i>	Juvenile	10	0	0	16	0	0	26	0	0
	Subadult	40	9	22.5	28	4	14.3	67	13	19.4
	Adult	236	98	41.5	262	91	34.7	498	189	38.0
<i>P. gossypinus</i>	Juvenile	4	0	0	2	0	0	6	0	0
	Subadult	3	0	0	8	0	0	11	0	0
	Adult	37	12	32.4	26	4	15.4	63	15	23.8
<i>Sigmodon</i>	Juvenile	17	0	0	11	0	0	28	0	0
	Subadult	19	3	15.8	33	2	6.1	52	5	9.6
	Adult	57	16	28.0	52	23	44.2	109	39	35.8

mice and cotton rats. An age effect in infection rate also appears to persist into the adult class of *P. floridanus*. Thirty-one nonparasitized males from infected populations had a mean weight of 28.2 g, while mean weight of 28 parasitized males was 35.0 g. Corresponding values for 37 noninfected females and 12 infected females were 29.5 g and 34.7 g respectively. It thus appears that infections are more prevalent in older adults, assuming at least a rough correlation between weight and age in these field populations. With the exception of adult cotton rats, more males than females in each species and age group had *C. hepatica*. Although the differences are not statistically significant ($P > .05$) in any case, they are suggestive and may reflect larger activity ranges in males than females.

Seasonal variation in infections. Monthly infection rates in adult *P. floridanus*, *P. gossypinus*, and *Sigmodon* from one extensively sampled scrub locality (Levy-19) are shown in Text-fig. 4. The graphs are based on composite samples representing eight years of collecting and thus reveal only average trends. In the Florida mouse, infections appear to be relatively low during the winter months and to increase during summer and early fall. Although the data are limited, a similar seasonal trend is suggested for *P. gossypinus*. Peak levels of infection in *Sigmodon*, however, appear to come in the spring, although incidence during the winter months tends to be low as in the case of the two *Peromyscus* species.

Relationship between incidence and host density. Population levels and infection rates in two scrub populations of *P. floridanus* are compared in Table 5. The number of mice captured per 100 trap-nights is employed as the index of



TEXT-FIG. 4. Seasonal variation in adult infection rates at a single scrub station (Levy-19).

TABLE V
RELATIONSHIP BETWEEN POPULATION LEVEL AND INCIDENCE OF *C. hepatica* IN ADULTS
OF TWO *P. floridanus* POPULATIONS

Station 10				Station 19			
Month and year	Pop. index (mice/100 trap-nights)	N	Adult Inf. rate (%)	Month and year	Pop. index (mice/100 trap-nights)	N	Adult Inf. rate (%)
Jan. 1961	49*	12	16.6	May 1960	20*	10	70.0
Jan. 1962	53*	2	0	May 1961	28*	17	70.5
Feb. 1959	48**	10	0	May 1963	6*	7	85.7
Feb. 1961	91*	6	0	July 1957	5*	4	100.0
May 1957	26**	36	2.8	Aug. 1960	17*	9	80.0
May 1961	24*	7	14.3	July 1961	14*	7	75.0
Apr. 1962	51*	9	0	Oct. 1960	21*	11	66.6
May 1963	16*	8	62.5	Sept. 1961	2*	1	100.0
Aug. 1958	38**	10	10.0	Dec. 1960	17*	9	70.0
Aug. 1960	23*	5	0	Dec. 1962	10*	5	62.5

*Trapline with 2 traps/station
**100 ft. grid, 1 trap/station

mouse abundance. The combined data for the two localities suggest a negative correlation between host abundance and degree of parasitism in this species. Station 10, with an over-all population index of 42 mice per 100 trap-nights, had a mean infection rate of 10%, as compared to station 19 with a mean population index of 14 and an adult infection rate of 78%. A similar relationship is evident within each population when comparison is made between abundance and infection rates at the same season in different years.

DISCUSSION

This study indicates that *Capillaria hepatica* is a relatively localized and uncommon parasite of Florida mammals, yet probably is rather widely distributed in the state. While records were obtained from only three of the 22 counties in which collecting was done, these localities are widely separated, Levy and St. Johns Counties

being located on opposite sides of the northern part of the peninsula and Highlands County in the south-central part of the state.

Levels of infection previously reported in rodents in North America vary greatly (Table 6), although variations in sampling techniques and methods of reporting results make critical comparisons and interpretations difficult. In general, the present data suggest that the parasite occurs with greater frequency in *Rattus*, particularly urban populations, than in native species. Compared to other native rodents, the incidence of *C. hepatica* in the three Florida species is relatively high. This is particularly true of *P. floridanus* and *Sigmodon*. The greater infection rate given for the Florida mouse in this paper compared to that reported earlier (Layne & Griffo, 1961) is due to additional collecting of this species being concentrated in areas with higher rates of infection. This in itself illustrates the

TABLE VI
REPORTED INFECTION RATES OF *C. hepatica* IN NORTH AMERICA RODENTS

Species	Locality	Incidence, per cent	Source
<i>Sciurus niger</i>	Louisiana	3.7	McQuown, 1954
<i>Peromyscus maniculatus</i>	Ontario	9.4	Freeman & Wright, 1960
<i>P. maniculatus</i> *	Washington	"virtually all"	Dalquest, 1948
<i>P. floridanus</i>	Florida	2.9	Layne & Griffo, 1961
<i>P. floridanus</i>	Florida	15.4	Present study
<i>P. gossypinus</i>	Florida	6.3	Present study
<i>Sigmodon hispidus</i>	Florida	10.5	Present study
<i>Clethrionomys gapperi</i>	Ontario	2.8	Freeman & Wright, 1960
<i>Ondatra zibethicus</i>	Louisiana	less than 10-ca. 50	Penn, 1942
<i>O. zibethicus</i>	Maine	17+	Meyer & Reilly, 1950
<i>O. zibethicus</i>	Michigan	3	Ameel, 1942
<i>Mus musculus</i>	Maryland	4	Luttermoser, 1938
<i>Rattus norvegicus</i>	Quebec	6	Firlotte, 1948
<i>R. norvegicus</i>	Maryland	85.6	Luttermoser, 1936
<i>R. norvegicus</i>	Maryland	47.9	Shorb, 1931
<i>R. norvegicus</i> (semi-wild)	Maryland	53.3	Calhoun, 1962
<i>R. norvegicus</i> (semi-wild)	Maryland	35	Habermann <i>et al</i> , 1954
<i>R. norvegicus</i>	Maryland	94.1	Davis, 1951
<i>R. norvegicus</i>	New York	73.5	Herman, 1939
<i>R. norvegicus</i>	Pennsylvania	<30	Herman, 1939
<i>R. norvegicus</i>	North Carolina	2.6	Harkema, 1936
<i>R. norvegicus</i>	Washington, D. C.	77	Price, 1931
<i>R. norvegicus</i> (396) + <i>R. rattus</i> (4)	Panama	12	Calero <i>et al</i> , 1950

*Parasite not identified in paper but from description almost assuredly *C. hepatica*.

problems involved in attempting to assess the real significance of differences in incidence values given by various authors.

Herman (1939) noted that few of the infected *Rattus norvegicus* examined from the New York Zoological Park had the entire liver affected by lesions and that in only 14% was more than half of the organ involved. Luttermoser (1936) similarly observed that infections in Baltimore rats were of low intensity. Assuming generally comparable criteria of extent of infection in the above and present studies, both Florida mice and cotton rats appear to have a greater proportion of heavy infections than *Rattus*. Dalquest (1948), presumably referring to *C. hepatica*, stated that virtually all *P. maniculatus* collected on Jones Island in the San Juan Island group off the coast of Washington had greatly swollen livers with a yellow, crystalline appearance. This description would appear to fit the category of heavy infection as used in this study. These limited data suggest that native rodents may tend to acquire more intense infections of *C. hepatica* than *Rattus*.

An earlier study (Layne & Griffo, 1961) revealed *C. hepatica* to be almost entirely confined to populations of the Florida mouse living in scrub or similar habitat types. The present data, representing numerous other potential host species and more extensive locality and habitat sampling, provide further confirmation of a highly restricted ecological distribution for this parasite in Florida. All of the infected specimens of the three host species were collected in scrub or similar habitats or from other habitats located near scrub from which infected animals could readily disperse. The over-all incidence of infection in each species also is clearly correlated with the extent to which it is found in scrub habitats. Of the three species, the Florida mouse is most characteristic of scrub and has the highest incidence of *C. hepatica*. Cotton mice and cotton rats occur more commonly in other habitats. In the present study, cotton rats were more abundant in scrub than cotton mice. In addition, live trapping data from permanent study plots indicated that cotton rats living in scrub tend to be more sedentary than cotton mice, many of the latter trapped in this habitat appearing to be transient individuals. This may explain the relatively low incidence and intensity of *C. hepatica* infections in *P. gossypinus* even from scrub stations with unusually high incidence of the parasite in *P. floridanus* and *Sigmodon* populations.

The pronounced habitat specificity of *C. hepatica* in Florida is not evident in other parts of the species' range. Rather, the great ecological diversity represented by its known hosts in North

America (Table 1) and elsewhere together with its extensive geographic range suggest broad environmental tolerance. Furthermore, specific information on habitat relationships in other parts of the range indicates that, unlike the case in Florida, the parasite tends to have higher prevalence in more moist habitat types (Freeman & Wright, 1960; Pavlov, Skrijabin *et al.*, 1957, cited from Freeman & Wright, 1960).

The basis of the marked restriction in the ecological distribution of *C. hepatica* in Florida is far from clear. Among the factors that might be involved are distribution of suitable hosts, substrate characteristics, host population dynamics, methods of egg-release and dissemination, and feeding habits of potential hosts.

There does not appear to be any strong correlation between the ecologic distribution of *C. hepatica* and mammalian hosts in Florida. The wide variety of known hosts of this parasite indicate that any of the small rodents involved in this study would serve as a suitable host. Moreover, the species often found infected in scrub or similar habitats also commonly occurred singly or in combination in other habitat types from which *C. hepatica* was only rarely or never recorded. In a number of cases such habitats were actually continuous with scrub with a high incidence of the parasite.

It is possible that scrub soils provide better conditions for survival or embryonation of eggs released from livers of the host than those of other habitats included in this survey. In view of the wide geographic range of the parasite and the variety of its recorded hosts, it does not seem likely that substrate conditions would have such an important influence on its ecologic distribution in Florida. Furthermore, if substrate conditions are so critical, it is difficult to reconcile the evidence for preferences for moist conditions in other parts of the range with high incidence in very sandy, highly drained soils in Florida. The picture is further complicated by the fact that *C. hepatica* appears to be completely absent from longleaf pine-turkey oak woodlands which are also characterized by sandy, well-drained soils, although there are important structural and chemical differences between the soils of these habitats and true scrub.

Freeman & Wright (1960) believed that population density played an important role in determining the incidence of *C. hepatica* in small rodents in a local area in Ontario. Although host population level may be an important factor influencing establishment or persistence of *C. hepatica* in certain habitats included in this study, there is no convincing evidence that it is a major cause of the observed habitat distribu-

tion of the parasite. Scrub and related habitat types in which infections occurred did not consistently support higher populations of small rodents than other habitats from which infections were never reported; nor does there seem to be any significant correlation between host abundance and infection rate at different stations in scrub habitat. In fact the data suggest an inverse relationship. On the other hand, small rodents are often scarce in longleaf pine-turkey oak woodlands, and although other aspects of the habitat might be suitable for *C. hepatica*, the low host density might make establishment and maintenance of the parasite difficult. Opposed to this argument, however, is the fact that some of the scrub habitats and the single slash pine-turkey oak woodland station studied over a period of several years at times had populations as low or lower than some longleaf pine-turkey oak stations yet maintained relatively high levels of *C. hepatica* infections. Possibly the interval of host scarcity is the critical factor in this situation; evidence indicates that periods of continuous low population density may be considerably more prolonged in longleaf pine-turkey oak habitats.

Laboratory studies on the life cycle of *C. hepatica*, reviewed by Freeman & Wright (1960) and Wright (1961), indicate that infections are acquired through ingestion of infective ova released from the liver of another host through cannibalism, predation, or natural death and decomposition. Ova freed through decomposition of the liver require a longer period for embryonation and have lower viability than those passed through the alimentary tract of another animal.

Although little is known of the actual details of the life cycle under natural conditions, it is logical to assume that cannibalism and predation are the most important of the commonly accepted egg-disseminating mechanisms. Freeman & Wright (1960) concluded that cannibalism in communal winter nests, rather than predation, was the chief source of infections in deer mice in Ontario, although their evidence was entirely circumstantial and subject to other interpretations.

Cannibalism does not appear to be an important egg-releasing mechanism in Florida mammals. Field data provide no evidence of communal nesting or cannibalism in any of the three host species, nor is there any reason to suppose that if these phenomena were common they would be more prevalent in scrub than other habitat types in which the species are found. This leaves predation as the more likely method of egg-dissemination.

All other things being equal, higher predation

levels would seem to contribute to maintaining *C. hepatica* in a small mammal population by insuring a continuous supply of infective ova. Present data are far too limited to allow definitive conclusions concerning relative predator abundance in the various habitats sampled. However, casual observations gave the impression that potential small mammal predators such as bobcats, foxes, raccoons, opossums, skunks, feral pigs, snakes, and birds of prey tended to be more common in scrub than in many of the habitats studied. In fairness, it should be noted that predator sign was probably more easily observed in scrub than in some of the other habitats studied. As in the case of rodent population levels, however, abundance of potential predators was by no means associated only with scrub habitats and thus cannot fully explain the high incidence of *C. hepatica* there. Furthermore, as some of the scrubs with high incidence of *C. hepatica* were small, many of the vertebrate predators occurring there probably ranged over other habitat types in the vicinity, thus providing opportunity for wider dispersal of ova from infected rodents eaten.

Certain aspects of the feeding behavior of Florida mice, cotton mice, and cotton rats in scrub seemed to be more specific to this habitat type than the factors mentioned above. The two *Peromyscus* species are essentially granivorous in their dietary whereas the cotton rat is typically herbivorous. However, field observations indicate that all three species have generally similar feeding habits when living in scrub. Acorns appear to be an important food source in scrub. They are generally abundant in late fall and early winter and decline steadily through winter and spring. The rodent populations follow the same annual cycle of abundance and decline. As mast supplies become scarce in late winter and spring, there is much evidence of digging by the rodents for food. This behavior would seem to increase the probability of exposure to infective ova in the soil.

A preliminary attempt to obtain actual evidence for this hypothesis in a scrub habitat (Levy—19) with an unusually high level of *C. hepatica* was unsuccessful. Fifty soil samples from the surface to a depth of about 2 inches were collected, many from within and around pits dug by foraging mice, and examined microscopically for ova. In addition, feces and stomach contents of 30 *P. floridanus*, the species with the highest incidence of infections at this station, were also surveyed for eggs in the hope that the presence of ingested eggs together with food remains would provide some clue to the source of infections. No ova were detected in either case.

None of the above factors seems adequate alone to account for the narrow habitat specificity of *C. hepatica*. It is possible, therefore, that the ecologic distribution of *C. hepatica* is due to a particular combination of such factors which has a much higher probability of occurrence in scrub than other habitat types. This set of conditions might include 1) substrate suitable for survival of ova, 2) sufficiently stable and high enough populations of potential host species to insure continuance of the cycle of parasitism, 3) an abundant enough supply of small mammal predators to insure an adequate supply of infective ova, and 4) host foraging behavior conducive to exposure to ova. Although this explanation is more consistent with the present data than a single factor model, it is still difficult to conceive of an interaction of a number of factors being responsible for the sharply delimited habitat distribution of *C. hepatica*. Thus, although such a combination of conditions as noted above may be generally prerequisite for the occurrence of the parasite, some additional feature unique to scrub and related habitats may actually be the critical factor permitting its establishment and maintenance.

Such a factor may be the presence of some invertebrate species, most likely an insect, in scrub habitats which may play a key role in the transmission of the parasite. It may supplement or replace vertebrate predators as the chief egg releasing and disseminating agent through feeding on dead mice or on feces of predators which have eaten infected mammals. It may increase probabilities of accidental ingestion of *C. hepatica* eggs by potential hosts simply by contributing to broader dispersal of infective eggs in the soil through its feces, or may be an even more effective agent in maintaining the host-parasite cycle through actually inhabiting and contaminating the nests of rodents. It is also possible that mice might acquire infections directly by feeding on the insect, particularly in times of food shortage. The suggestion of seasonal variation in incidence of infections shown by the present data is of interest in this connection. In all host species, peak levels tend to occur in the spring or summer months and low rates during the winter months. Higher incidence thus correlates with both a period of food scarcity in which rodents might take more insects and warm weather favoring insect activity.

With the exception of a study by Momma (1930), the possible role of insects or other invertebrates in dissemination of ova of *C. hepatica* appears to have been ignored. Momma experimentally demonstrated that flies exposed to *C. hepatica* eggs both ingested and picked them

up on the body and that the ova embryonated normally after passage through the intestine of the insect. He concluded that high summer and low winter infection rates in *Rattus norvegicus* in urban areas of Japan, together with low incidence of eggs (in only 5 of 503 specimens examined) in intestines of cats used for rat extermination, was evidence that flies were the primary method of egg dissemination.

SUMMARY

A total of 2,254 specimens of 27 species of Florida mammals was examined for infections of the liver-inhabiting nematode *Capillaria hepatica* (Bancroft, 1893). Collections were made in 22 counties of the state and in nine major habitat types.

Infections were recorded in three rodents, *Peromyscus floridanus*, *P. gossypinus*, and *Sigmodon hispidus*, from three widely separated localities. *P. gossypinus* constitutes a new host record for the parasite and *Sigmodon* a new record for Florida and the southeastern U.S. generally.

Over-all incidence of infection was 15.4% in *P. floridanus*, 6.3% in *P. gossypinus*, and 10.5% in *Sigmodon*. Prevalence in *P. floridanus*, *P. gossypinus*, and *Sigmodon* from stations positive for infections in any species was 34.2%, 14.8%, and 21.1%, respectively. Severity of infections was greater in *P. floridanus* and *Sigmodon* than in *P. gossypinus*.

Infections were largely restricted to scrub and related habitats, the rare occurrences in other major habitat types in most cases being explainable on the basis of dispersal of infected animals from scrubs. The basis of the narrow habitat specificity of the parasite in Florida, which is not apparent in other parts of its range, is unknown. Such factors as host distribution, substrate conditions, host and predator population levels, and feeding habits of hosts do not, either singly or in combination, appear to adequately account for the marked restriction of the parasite to scrub environments; and the possibility of some insect being the key factor is suggested.

In all three host species, infection rates were greater in older age classes, and in all age groups males tended to have a higher infection rate than females, although these differences were not statistically significant. Although seasonal variation in infection rates was not pronounced, incidence tended to be low in all species during the winter months, with peak levels occurring in spring in *Sigmodon* and summer in the *Peromyscus* species. Population levels and incidence of parasitism in two scrub populations exhibited an inverse relationship.

A summary of North American host and locality records of *C. hepatica* is provided.

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EXPLANATION OF THE PLATE

PLATE I

- FIG. 1. Normal liver of *P. floridanus* (left) and one showing lesions of *Capillaria hepatica* (right). Note lobulation of infected liver.
- FIG. 2. Ovum of *Capillaria hepatica* from liver of *P. floridanus*. X625.
- FIG. 3. Ova of *C. hepatica* in liver of *P. floridanus*. X300.



FIG. 1



FIG. 2

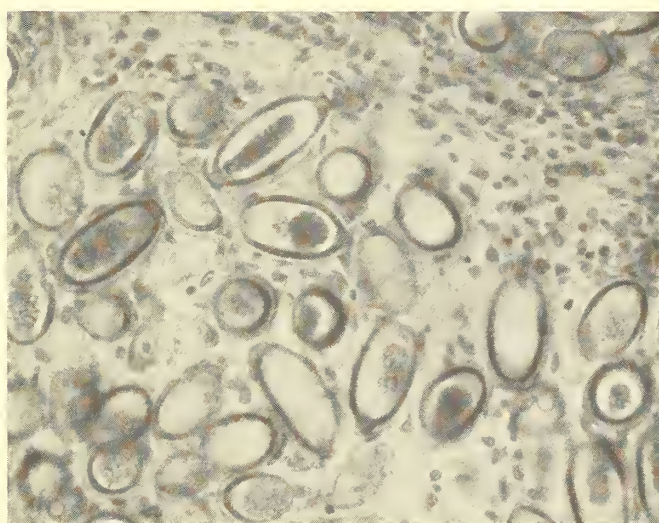


FIG. 3

HOST AND ECOLOGICAL RELATIONSHIPS OF
THE HELMINTH *CAPILLARIA HEPATICA* IN FLORIDA MAMMALS

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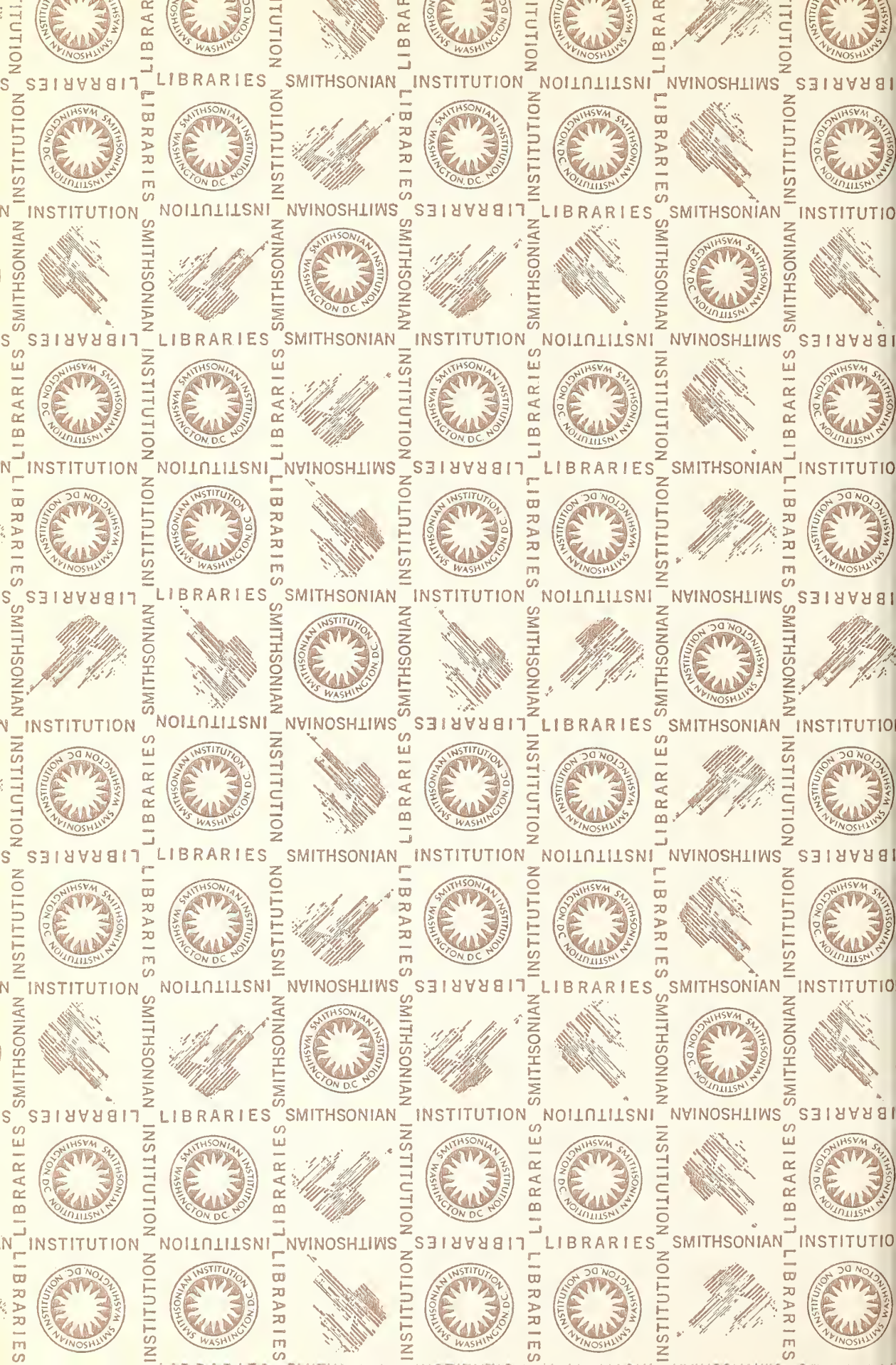
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